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RECLASSIFICATION OF THE REPTILIA.

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HISTORY OF CLASSIFICATION.<sup>1</sup>

*Philosophy of Classification.*—The history of the classification of the Reptilia resembles that of the classification of other forms of vertebrates in its gradual approximation to the truth.

The general progress has been from superficial to profound characters, from purely adaptive characters to those which are phylogenetic and indicate real affinity. For a century and a half superficial resemblances and analogous adaptations have been the pitfalls out of which the final classification is slowly emerging.

Every classification, moreover, has had its underlying philosophy. The "special creation" philosophy underlays the Linnæan system, but in so far as Linnæus, Cuvier, De Blainville, Owen perceived a real order in certain profound characters, their systems will stand.

The philosophy underlying modern classification is the

<sup>1</sup> Presented at the first meeting of the Society of Vertebrate Palæontologists, Philadelphia, December 29th, 1903. Abstract, in part, of a memoir entitled The Reptilian Subclasses Synapsida and Diapsida and the Early History of the Diaptosauria. *Mem. Amer. Mus. Nat. Hist.* Vol. I, Pt. VIII, Nov. 1903.

Lamarck-Darwin theory of the law of descent which involves a branching or phylogenetic scheme of relationships. Toward this we are slowly progressing. The final classification will be a formal or tabular statement of the tree of descent, in which only so much pre-Darwinian classification will survive as was based upon the perception of real phylogenetic characters.

The evolution philosophy held out a strong temptation to rapid generalization in phylogeny. It is a striking fact that the evolutionists, Huxley, Cope, Hæckel, perhaps because they attempted to generalize too rapidly, have proved less fortunate in their arrangement of the Reptilia than Owen, whose pre-Darwinian systems of 1839 and 1859 have best stood the test of time and of discovery.

Both Cope's and Huxley's systems are largely wrecks today; Huxley's because while entirely logical in method it outran the state of knowledge and discovery. Cope was less logical; his fatal error was over reliance on single characters without discriminating whether they were primitive or adaptive. Marsh was gifted with unerring taxonomic judgment as to real phylogenetic relationships; the chief defect of his system was that he partly or wholly ignored the rules of priority, renaming and redefining groups which had previously been defined with sufficient clearness to be recognized. It is with real regret that I feel compelled, as a matter of historic justice, to revive some of the older names for certain groups of which our knowledge is almost entirely due to the fundamental contributions of Marsh.

*Priority.*—Palæontological discovery is constantly swelling and expanding the groups of fossils discovered long ago; it is consequently necessary either to abandon these groups or to raise or lower their grade. For example, Owen's "family" Cynodontia has become a suborder, his "families" Dicynodontia and Theriodontia have become orders, his "orders" Anomodontia and Dinosauria have become superorders.

If we should confine each group to the rank or systematic position originally assigned to it by its author in a very limited state of knowledge, we should have to rename the larger number of groups, and this certainly is not advisable either in the interest of clearness or as a matter of historic justice.

The history of classification is usually presented by giving the complete schemes published successively by various anato-



FIG. 1.—A primitive Plesiosauroid Synapsidan, *Lariosaurus balsami*. After Boulenger.  $\times \frac{1}{2}$ .

mists. The student will perhaps gain as valuable a lesson by considering the anatomical philosophy, true or false, which has prompted different systems of classification.

## FALSE PRINCIPLES OF CLASSIFICATION.

*Superficial Resemblances.*—In Brogniart's system of 1799 the Lacertilia and Crocodilia are wrongly united on limb structure as (II) Saurii, as distinguished from (III) Ophidii, and (I) Chelonii.

The similar scaly covering led Latreille (1820) to rightly unite the Ophidia and Lacertilia as Squamosa; previously Oppel (1811) grouped the Lacertilia and Ophidia as Squamata; this, however, is the single instance in which epidermal resemblance happens to coincide with underlying fundamental characters.

As instances of errors based upon epidermal characters, we may cite the union of the Testudinata and Crocodilia by Klein as Cataphracta; or the union of the same animals by Merrem as Loricata.

*Resemblances in Single External Organs.*—So able a palæontologist as von Meyer (1830) attempted to classify the reptiles by resemblances in foot structure. He thus divided the Saurii, or limbed reptiles into (1) Dactylepodes, including Lacertilia and Crocodilia; (2) Nexipodes, including the Ichthyosauria and Sauropterygia (*Plesiosaurus*, *Nothosaurus*); (3) Pachypodes, including the Iguanodontia and Megalosauria; (4) Pterodactylii, including the Pterosaurs—a false system.

*Classification of Analogous Adaptations.*—De Blainville (1835) united the Ichthyosauria and Sauropterygia as Enaliosaurii, or sea lizards. Owen (1839) adopted the order Enaliosauria as embracing the Ichthyopterygia (1859) and Sauropterygia (1859), but remarked that these animals “do not form a strictly natural group.”

*Classification by single Internal Characters.*—This method was especially characteristic of Cope. In 1869 he defined the Archosauria as differing from the Monimostylica of Müller only by the exclusion of the order Testudinata; he observed that close sutural attachment of the quadrate bone “was the important feature which characterizes the order”; by this feature he united the Sauropterygia (*Nothosaurus*, which was selected as a type) the Crocodilia, the Thecodontia (suborder of Dinosauria), the Dinosauria, the Anomodontia, and the Rhynchocephalia; a totally unnatural and transitory grouping, because based upon



the possession of a single primitive character, namely, the *fived quadrate*.

We find that almost every attempt to classify the reptiles by superficial characters, by external organs, by general external adaptations, by single internal organs, has proved unnatural.

#### TRUE PRINCIPLES OF CLASSIFICATION.

The conclusion is that there are three ruling principles in classification.

First, as to *priority*, we owe it to our palæontological forebears not to abandon the lower or higher groups they have proposed except in cases of absolute necessity. In some instances we must give a group a higher or lower rank than the author originally assigned to it, or a different position in the system. Priority has no force where a group is based on a false conception or on a false grouping of types, as in the definitions of Theromorpha and Archosauria by Cope.

Second, as to *phylogeny*, classification is a formal expression of our knowledge of phylogenetic relationships; it must, therefore, constantly shift and change as new relationships are discovered. The final classification will be the phylogenetic tree. This being the case, it is desired to include within a group its ancestral forms as soon as they have definitely branched off toward it. For example, Hyracotherium should not be placed in the Lophiodontidæ, as was done by Cope, but in the Equidæ. Again, if it should be demonstrated that the Protorosauria are ancestral to the dinosaurs and to no other reptiles, they should be placed in the superorder Dinosauria.

Third, as to *definition*, classification, like phylogeny, should be based on a number of characters of different parts of the body having different functions, in order to diminish the danger of being misled by analogous evolution, otherwise known as parallelism, convergence and homoplasy.

The neglect of one or other, and in some cases of all these three principles and the loss of the clarifying mind of George Baur have led to great and rapidly increasing confusion in the arrangement of the Reptilia in recent years. Smith Woodward, Broom and von Nopsca, have been working in the right direction.

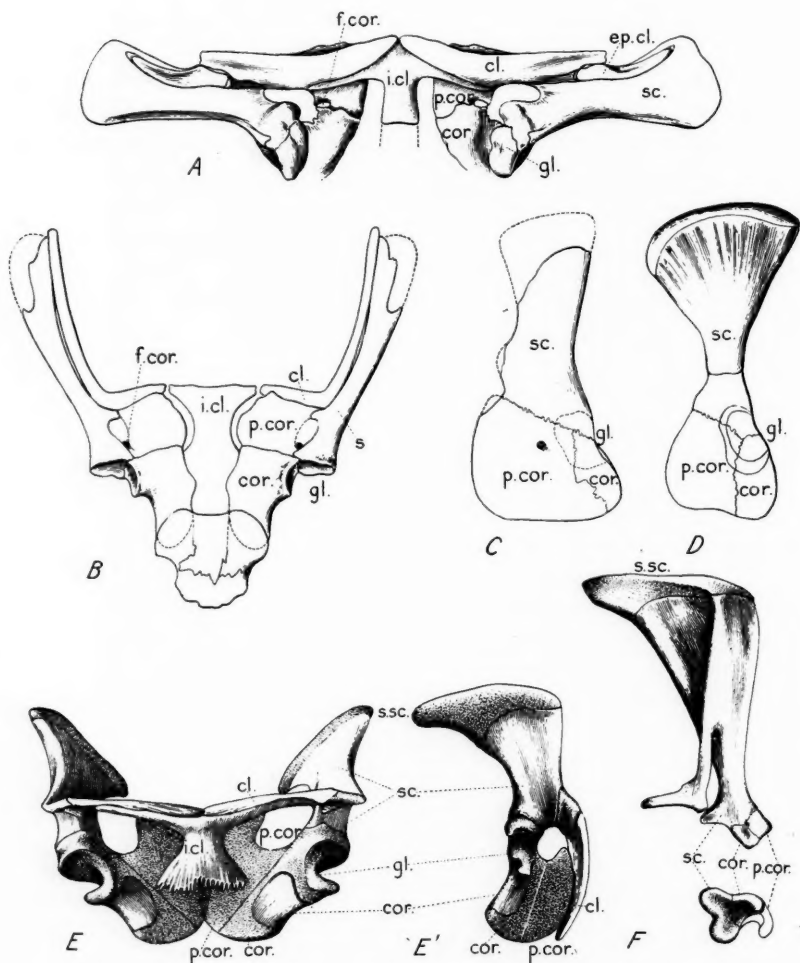


FIG. 2.—Synapsidan and mammalian types of shoulder-girdle. A-D, after Seeley; E-F, after Howes. A, *Paraciaurus bainii*; B, *Kerogonathus cordylus*; C, *Deuterosaurus*; D, *Rhopalodon*; E, ventral, E', lateral views of *Ornithorhynchus*; F, *Lepus*.

## PROPOSED RECLASSIFICATION.

At the Washington meeting, 1902, of the American Association, I presented a joint paper with Dr. J. H. McGregor on the diphyletic arrangement of the reptiles, based on comparison of a large number of characters. I have since made a more searching study of the same problem, designating these two groups as the subclasses SYNAPSIDA, or primitively single-arched reptiles, and DIAPSIDA, or primitively two-arched reptiles, and have grouped all the most primitive forms of Diapsida in the superorder DIAPTOSAURIA, a group equivalent in taxonomic rank to the Squamata or the Dinosauria. I now propose to briefly describe the reptiles which fall within these two groups.

## SUBCLASS SYNAPSIDA Osborn.

The chief distinction of the single arched reptiles is that there is either no opening at all in the temporal region (Cotylosauria), or a single large supratemporal opening (Anomodontia, Plesiosaurs, Testudinata) as in the upper view of the skull of a plesiosaur, a turtle, or a mammal. This supratemporal fossa is large, because the cranium or brain case is long while the facial portion of the skull is relatively short, these proportions being directly reversed in the Diapsida. The temporal arch consists primitively of two arches combined. The squamosal is always a large element. The quadrate is correspondingly more or less reduced; it is never movable, and is functionally supported by the squamosal. In the shoulder girdle the coracoid and procoracoid are separate, or united by suture. The phalangeal formula is primitively 2. 3. 3. 3. 3, like that of mammals.

I. *Order* COTYLOSAURIA Cope

## Pareiasauria Seeley.

These are the most primitive of reptiles, retaining many Stegocephalian (amphibian) characters, and a solid cranial roof with temporal openings rudimentary or not developed at all.

Subclass **SYNAPSIDA** Osborn 1903.  
 Order **COTYLOSAURIA** Cope 1880  
 (Pareiasauria Seeley 1889)  
 Superorder **ANOMODONTIA** Owen  
 1860. (Theromorpha Cope 1878, in  
 part.)  
 { Order **THERIODONTIA** Owen 1876.  
 Suborder **Therocephalia** Broom  
 1903.  
 Suborder **Cynodontia** Owen  
 1861.  
 Order **DICYNODONTIA** Owen 1860.  
 Order **PLACODONTIA** *auct. ex* H.  
 von Meyer<sup>3</sup> 1863 *Incertæ Sedis*.  
 Order **SAUROPTERYGIA** Owen 1860.  
 Suborder **Simosauria** *auct. ex*  
 Gervais<sup>1</sup> 1845.  
 (Nothosauria Seeley 1882.)  
 Suborder **Plesiosauria** *auct. ex*  
 Quenstedt<sup>2</sup> 1852.  
 Order **TESTUDINATA** *auct. ex*  
 Shaw<sup>4</sup> 1802.  
 Suborder **Pleurodira** *auct. ex*  
 Duméril and Bibron<sup>5</sup> 1835.  
 Suborder **Cryptodira** *auct. ex*  
 Duméril and Bibron<sup>6</sup> 1835.  
 Suborder **Trionychia**<sup>7</sup> *auct. ex*  
 Pictet 1853.

<sup>1</sup> "Simosauriens."

<sup>2</sup> "Plesiosauri."

<sup>3</sup> "Placodonten."

<sup>4</sup> "Testudines."

<sup>5</sup> "Pleurodères."

<sup>6</sup> "Cryptodères."

<sup>7</sup> "Trionychides."

<sup>8</sup> "Mosasauridés."

<sup>9</sup> The dates and authors assigned for the earliest recognition of the supergeneric rank of several of these groups may be altered by future investigations.

Subclass **DIAPSIDA** Osborn 1903.  
 Superorder **DIAPTOSAURIA** Osborn  
 1903.

{ Order **PROCOLOPHONIA** Seeley  
 1867.  
 Order **PROTOROSAURIA** Seeley  
 1887.  
 Order **PROGANOSAURIA** Baur 1887.  
 Order **GNATHODONTIA** Owen 1860.  
 (Rhynchosauria Osborn 1903).  
 Order **PELYCOSAURIA** Cope 1878.  
 " **CHORISTODERA** Cope 1877.  
 " **RHYNCHOCEPHALIA** Gün-  
 ther 1868.  
 Order **PARASUCHIA** Huxley 1875.  
 Suborder **Aëtosauria** Nicholson  
 and Lydekker 1889.  
 Suborder **Phytosauria** Baur 1894  
*ex* Jaeger 1828.  
 Order **ICHTHYOSAURIA** Blainville  
 1835 *ex* Jaeger 1824.  
 (Ichthyopterygia Owen 1860.)  
 Order **CROCODILIA**<sup>9</sup> Wagler (?)  
 1830.  
 Suborder **Mesosuchia** Huxley  
 1875.  
 Suborder **Eusuchia** Huxley 1875.  
 " **Thalattosuchia** Fraas  
 1901.

Superorder **DINOSAURIA** Owen  
 1840.

{ Order **THEROPODA** Marsh 1881.  
 Suborder **Megalosauria** *ex* Fitz-  
 inger 1843.  
 (Thecodontia Owen 1860.)  
 Suborder **Symphypoda** Cope  
 1867.  
 (Compsognatha Huxley 1870.)  
 Order **OPISTHOCELIA** Owen 1860.  
 (Sauropoda Marsh 1881.)  
 Order **ORTHOPODA** Cope 1866.  
 (Predentata Marsh 1894.)

Superorder **SQUAMATA** Oppel 1811.

{ Order **LACERTILIA**<sup>9</sup> Owen 1839.  
 Order **MOSASAURIA** *auct. ex* Ger-  
 vais<sup>8</sup> 1845.  
 Order **OPHIDIA**<sup>9</sup> Brogniart 1802.  
 Order **PTEROSAURIA** *auct. ex* Kaup  
 1834.

The large South African Pareiasauridæ are more specialized than the Texan Pariotichidæ and Diadectidæ, the latter being the type of the order.

Theoretically some unspecialized members of this order gave rise to all other reptiles including both Synapsida and Diapsida.

## II. *Superorder* ANOMODONTIA Owen.

This was originally defined by Owen (1860) as an 'order' embracing the "families" Dicynodontia, Cryptodontia and Gnathodontia (*Rhynchosaurus*). The reference of the latter 'family' proves to have been an error. In 1861, in the second edition of his *Palæontology*, Owen included in the Anomodontia the 'family' Cynodontia, based on the types *Galesaurus* and *Cynochampsia*; thus raising the Anomodontia to the rank of a superorder which is equivalent in part to the superorder *Theromorphia* Cope.

This 'superorder' includes two orders, which represent an adaptive radiation from more primitive truly reptilian types (*Therocephalia* Broom) into the more mammal-like Cynodontia, both with full sets of teeth, and finally into the highly specialized Dicynodontia, in which the teeth are greatly reduced. All these animals retain, however, some primitive or cotylosaurian and stegocephalian characters.

### I. *Order* THERIODONTIA Owen.

#### 1. *Suborder* Therocephalia Broom.

Broom has recently published an admirable paper on the "Classification of the Theriodonts and their Allies,"<sup>1</sup> in which the Therocephalia<sup>2</sup> are defined from the types *Scylacosaurus*, *Ælurosaurus*, *Ictidosuchus*, *Deuterosaurus*, *Titanosuchus*, *Gorgonops*, as representatives of six families. These are medium sized reptiles, and apparently the most primitive of the Anomo-

<sup>1</sup> *Rep. So. Afr. Assoc. Adv. Sci.* 1903, pp. 362-369.

<sup>2</sup> This is defined as an order by Broom and may prove to be of full ordinal rank; it is here provisionally grouped with the Anomodontia as a suborder of Theriodontia.

dontia. The teeth are differentiated as in mammals into incisors, canines (sometimes double), and molars; the molars, however, are simple, and the palate is simple, like that of the Cotylosauria, that is, there is no secondary palate.

## 2. Suborder Cynodontia Owen.

This was originally defined as the "family" Cynodontia by Owen in 1861, and may be embraced within the order "Therio-

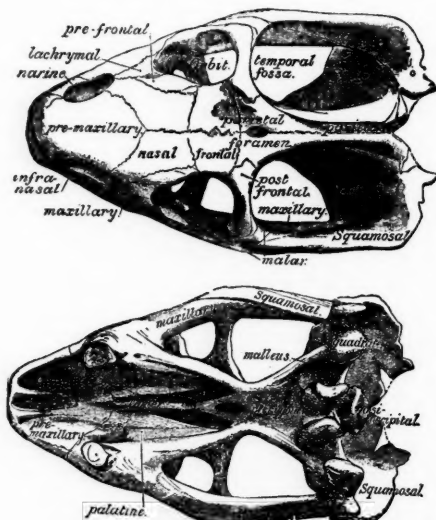


FIG. 3.—Synapsid Type. Palatal and superior views of the skull of *Dicynodon*, showing the elements as interpreted by Seeley. Note especially the exposure of the prevomer, the large extension of the squamosal, the pre- and postfrontals, the single squamoso-maxillary bar. After Seeley.

dontia" Owen of 1876, which was based on the same types, viz.: *Galesaurus* and *Cynochampsia*.

These are intermediate anomodonts of medium size. In contrast with the *Therocephalia* the squamosal is more expanded and the quadrate is greatly reduced. Approaching the mammals also, there is the secondary palate, formed of the maxillaries and palatines, also the double condition of the occipital condyles

which are single in Therocephalia. These cynodonts have lost several of the other more primitive characters of the therocephalians, such as teeth in the palate; and their specialization is in the direction of the mammalia. The phalangeal formula is 2. 3. 3. 3. 3. They include three families, typified respectively by the genera *Lycosaurus*, *Cynognathus*, and *Gomphognathus*.

## 2. Order DICYNODONTIA Owen.

This term was originally used as a "family" term, under Anomodontia, by Owen in 1859; Huxley raised it to the rank of an order from the types *Dicynodon*, *Oudenodon*. The latter, Owen (1859) had placed in the "family" *Cryptodontia*, in reference to the absence of teeth. Despite the high specialization of the dentition, these animals retain the more primitive features of the single condyle, of the cleithrum or epiclavicle, of the large quadrates. On the other hand, like the cynodonts, they show a rudimentary secondary palate. They approach the mammals also in the loss of the prevomers and development of the vomer (parasphenoid).

In the most primitive family of *Endothiodontidae* one or more series of molar teeth are present on the maxillaries and dentaries; the interclavicle is a rounded plate as in the *Stegocephalia*. In the more specialized *Dicynodontidae*, maxillary teeth are absent, or present as a pair of tusks, and there are no teeth in the lower jaw; the interclavicle is elongated, and a cleithrum is present. The third family, *Lystrosauridae*, exhibits a small interclavicle, and no cleithrum. A fourth family, *Cistecephalidae* is doubtfully ranked here by Broom.

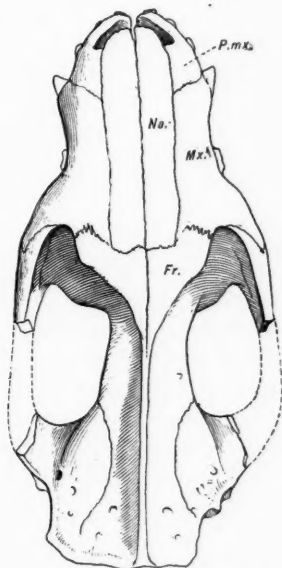


FIG. 4.—Synapsid Type. Top view of the skull of a primitive ambylopod ungulate, *Pantolambda*.  $\times \frac{1}{2}$ .

Broom has contributed a large number of papers on the structure and arrangement of the South African reptiles, which for the first time throw a perfectly clear light on their relationships to each other.

### 3. Order PLACODONTIA.

(*Incertæ sedis.*)

The position of this order as typified by the genus *Placodus*, is still very doubtful. It is characterized by very large teeth in the palate, and by the absence of teeth on the maxillaries and premaxillaries. It includes littoral, shell-eating forms, which may be an independent offshoot of the Anomodontia, or may be more nearly related to the Sauropterygia.



FIG. 5.—Synapsid Type. Dorsal aspect of skull of *Nothosaurus andriani*? A primitive plesiosauroid reptile. After Cope.

### III. Order SAUROPTERYGIA Owen.

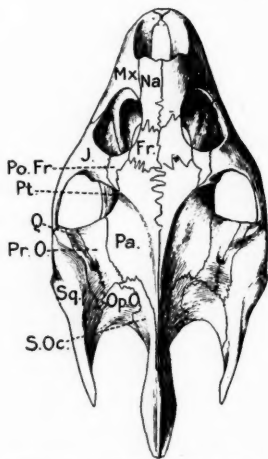


FIG. 6.—Synapsid Type. Dorsal view of skull of *Trionyx*.

The theory of the relationship of the plesiosaurs to the Synapsida and especially to the Anomodontia and Testudinata still requires confirmation. The skull structure is typically synapsidan. The shoulder girdle structure, so far as known, in the Triassic plesiosaurs is certainly more synapsidan than diapsidan. Numerous resemblances to the Testudinata have been pointed out. On the other hand, certain of the oldest Triassic plesiosaurs, such as *Lariosaurus*, (Fig. 1) closely approach the Diapsida in the phalangeal formula.



IV. Order TESTUDINATA (*ex* Shaw.)

The kinship of the Testudinata to the Synapsida is indicated both by the skull structure and by the phalangeal formula. The shoulder girdle structure, like that of the plesiosaurs, is still in dispute; the main question being as to the homologies of the

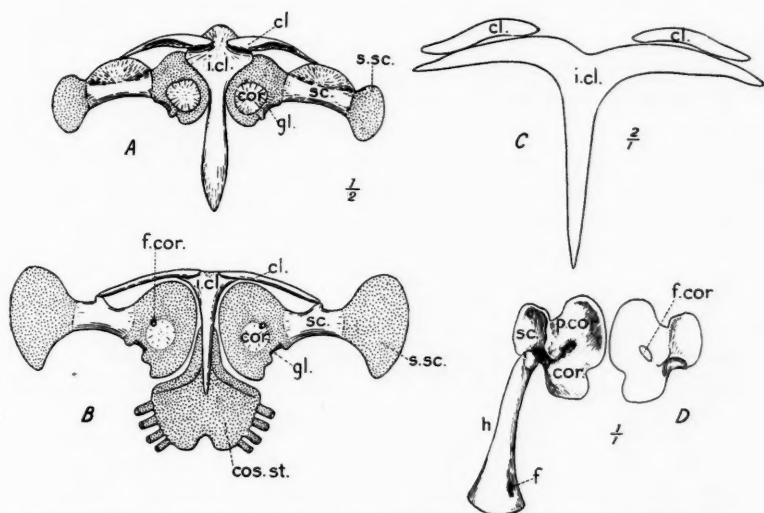


FIG. 7.—Diapsidan types of shoulder-girdle. *A*, Palæohatteria. After Credner. The cartilaginous areas are entirely restored. Restoration by J. H. McGregor.  $\times \frac{1}{4}$ . *B*, Sphenodon juv. (15 cm.); modified from Howes. By J. H. McGregor.  $\times \frac{1}{7}$ . *C*, Pleurosaurus. Cartilaginous elements omitted. After Dames.  $\times \frac{1}{7}$ . *D*, *Mesosaurus tenuidens*. Modified from Gervais.  $\times \frac{1}{7}$ .

*Cl*, clavicle; *i. cl*, interclavicle; *sc*, scapula; *s. sc*, suprascapula; *cor*, coracoid; *p. cor*, procoracoid; *f. cor*, coracoid foramen; *h*, humerus; *f*, entepicondylar (ulnocondylar) foramen.

anterior ventral processes variously known as the "procoracoid" or "proscapula."

## SUBCLASS DIAPSIDA Osborn.

All these animals are readily distinguished by their general likeness to the existing Hatteria. In contrast to the Synapsida the cranium is short; the temporal region is primitively fenestrated by two distinct openings, the supra- and latero-temporal fenestræ,

bounded by the supra and latero-temporal arches, one or both of which may secondarily disappear. In further contrast with the Synapsida, the squamosal is a relatively small element, frequently separate from the prosquamosal, and never entering into articulation with the lower jaw; the quadrate, on the other hand, is a relatively large element, uncovered, and sometimes secondarily movable. In the shoulder girdle we find a most distinctive character in the early coalescence of the coracoid and procoracoid into a single bone, or in the degeneration of the procoracoid. Another highly distinctive character is the phalangeal formula, 2. 3. 4. 5. 3-4, which is secondarily modified in the aquatic forms.

There appear to have been two great adaptive radiations among the Diapsida. The *first* is that which occurred during the upper Carboniferous and Permian, branches of which are

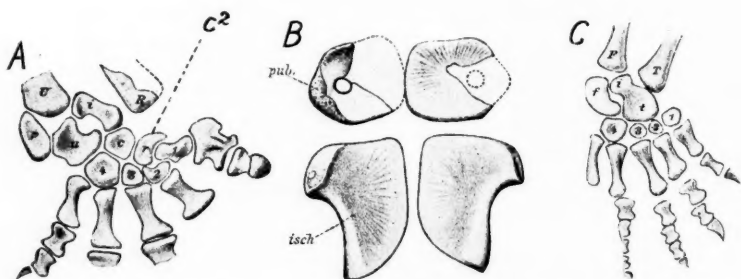
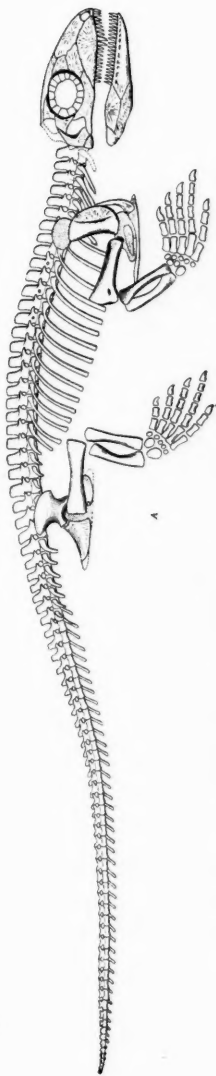


FIG. 8.—The most primitive known Diapsidan. *A*, manus, *B*, pubis and ischium, and *C*, pes, of *Procolophon trigoniceps* Owen (Order PROCOLOPHONTA). After Broom.  $\times \frac{1}{2}$ .

already well separated in the Permian and have been collectively grouped in the superorder Diaptosauria by Osborn. The *second*, or later radiation of the Diapsida, partly sprung from terminal branches of the first, is known in the Triassic, and includes the great orders Parasuchia, Ichthyopterygia, Crocodilia, the superorder Dinosauria, the superorder Squamata, and finally the Pterosauria.

I. *Superorder* DIAPTOSAURIA Osborn.

This superorder embraces the Rhynchocephalia of Günther, the Pelycosauria of Cope, which certainly represent distinct orders of reptiles, and the more or less distinct orders or suborders Protosauria, Procolophonia, Proganosauria, Choristodera, Gnathodontia, Rhynchocephalia. They have appropriately been termed 'rhynchocephaloid' reptiles by Broom.

The common characters of these primitive or stem Diapsida, are as follows: cranium with two complete temporal arches; vertebræ typically amphicoelous and often perforated by a notochordal canal; hypocentra frequently present throughout vertebral column; ribs on all vertebræ from first cervical to eighth caudal inclusive, generally single-headed or incipiently two-headed; large abdominal ribs or plastron always present; coracoid and procoracoid early uniting into a single bone; pubis and ischium ventrally in continuous contact or secondarily fenestrated.

The adaptive radiation of these mostly small sized animals into ambulatory, littoral, amphibious, and fully aquatic types, together with specializations of the skull and dentition for a great variety of feeding habits has resulted in a divergence sufficiently profound and ancient to form seven groups which have been variously assigned the rank of orders or suborders as follows:

FIG 9.—A primitive diapsidan. *Palaeohatteria longicaudata*. Restoration by J. H. McGregor.  $\times \frac{1}{2}$ . Order PROTOSAURIA.

## 1. Order PROCOLOPHONIA Seeley.

This includes the most primitive of the Diaptosauria; those closest to the Cotylosauria, and distinguished by the entire absence of lateroemporal fenestræ,<sup>1</sup> by the persistence of the epiotics and auditory notch of the cotylosaurs, and other very primitive characters. These animals are thus far recognized in the Permian of South Africa only.

## 2. Order PROTOROSAURIA Seeley.

This land group includes Protorosaurus, Palæohatteria, Kadaliosaurus, distinctively ambulatory and in part leaping reptiles, certainly carnivorous; distinguished by the straight limbs, strong development of the hind limbs, correlated with a dorsally expanded ilium and from two to three sacral vertebræ.

These animals show all the characters which we should expect to find in the ancestors of carnivorous Dinosauria; the three genera known are too far specialized in the direction of ambulatory and predatory types to have given rise to any of the other known Diaptosauria.

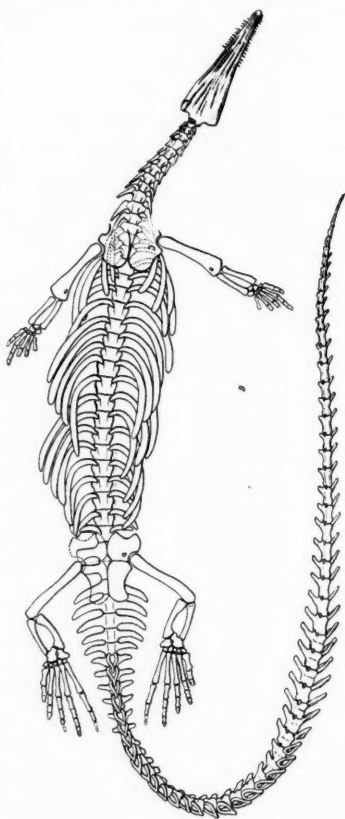


FIG. 10. *Stereosternum tumidum*. Restoration by J. H. McGregor.  $\times \frac{1}{4}$ . Order PROGANOSAURIA.

<sup>1</sup> Dr. R. Broom has just made this important observation.

## 3. Order PROGANOSAURIA Baur.

This aquatic or amphibious group, which has been confused with the Protorosauria, is at present represented only by the genera *Mesosaurus* Seeley and *Stereosternum* Cope, closely allied forms from the Permian of South Africa and South

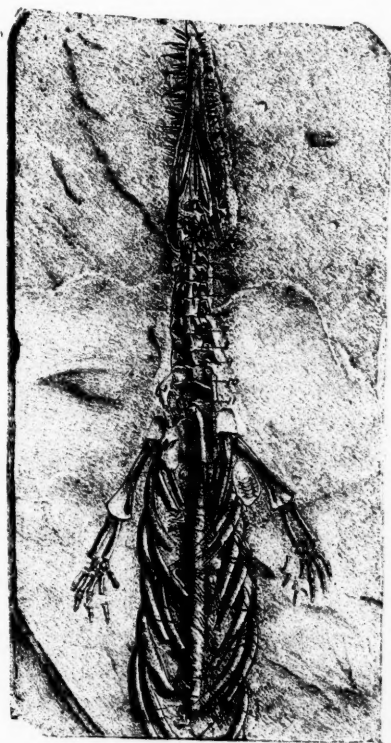


FIG. 10a.—*Mesosaurus tenuidens*. After Gervais.  $\times \frac{1}{2}$ . Order PROGANOSAURIA.

America. These are typical swimming or amphibious types, with greatly elongated rostrum, delicate, prehensile teeth, very heavy ribs with highly modified capitular attachments; the vertebræ are also highly distinctive and unique in structure.



the persistence in certain forms of a suture between the coracoid and procoracoid.

This line also became very highly specialized, and died out in the Trias.

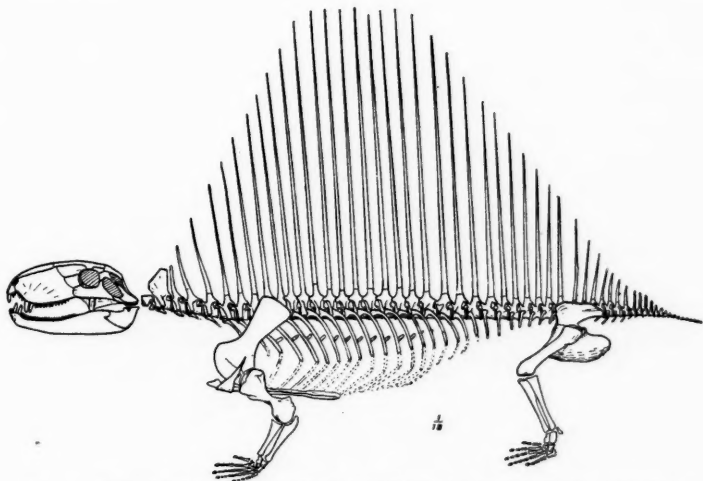


FIG. 12.—Restoration of *Embolophorus* (Order *PLYCOSAURIA*). About  $\frac{1}{18}$  nat. size. After Case.

#### 6. Order CHORISTODERA Cope.

These amphibious animals, found thus far only in the Cretaceous and in the Lower Eocene, represent a sharply defined division with a greatly elongated gavialoid rostrum, teeth acrodont and internally folded, dorsal ribs two-headed. They include the American *Champsosaurus* and the European *Simœdosaurus*; the latter being distinguished by more distinct adaptation to aquatic life were made the type of the order *Simœdosauria* by Dollo. The analogies are with the *Proganosauria* and the aquatic true *Rhynchocephalia*, but there are no phylogenetic relationships with these forms.

## 7. Order RHYNCHOCEPHALIA Günther.

These are the "Rhynchocephalia Vera" of Boulenger. They represent by far the most conservative of all the Diaptosauria because even the recent *Sphenodon* is in certain respects more primitive than most of its Permian relatives.

The order includes the Jurassic radiation of terrestrial, semi-aquatic, and fully aquatic types, with modifications paralleling

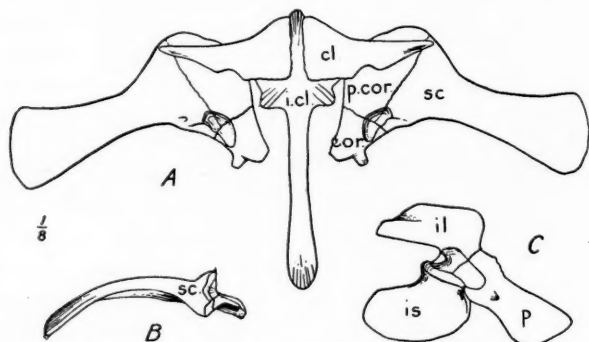


FIG. 13.—A. Shoulder-girdle of a Pelycosaurian (*Embolophorus*) B, Profile view of conjoined scapula and procoracoid of same. This is one of the few Diapsida in which the procoracoid is still separated by suture from the coracoid. C. Pelvis of same. After Case.  $\times \frac{1}{8}$ .

those in the Choristodera and Proganosauria, also the existing terrestrial genus *Sphenodon*. The Jurassic forms are in many respects less primitive than the existing genus.

## II. Order PARASUCHIA Huxley.

This amphibious fresh water group, typified by *Phytosaurus* and *Aëtosaurus*, placed in the suborders Aëtosauria and Phytosauria respectively, has long been treated in connection with the Crocodilia, owing to Huxley's influence and authority; McGregor has shown that it has practically no affinity to the Crocodilia, its relationships being closer to the Ichthyosauria, although it constitutes an independent order, probably of freshwater, littoral, carnivorous, short snouted (*Aëtosaurus*) or long snouted (*Phyto-*



saurus, *Mystriosuchus*) forms, analogous in their habits to the modern *Crocodylia*.

The *Parasuchia* are found by McGregor to represent an undoubted modification of the rhynchocephaloid or diaptosaurian type.

### III. *Order* ICHTHYOSAURIA Blainville.

The ichthyosaurs are also distinctively *Diapsida*, both in shoulder girdle and in basicranial structure. The latero-temporal fenestra, however, is closed, perhaps secondarily. The posterior position of the nares and the elongation of the snout in front, is analogous to that in the *Parasuchia* and may be indicative of divergence from a common stem.

The most primitive form, *Mixosaurus* affords a transition to the ambulatory limb type of the *Diaptosauria*. None of the known orders of *Diaptosauria*, however, can as yet be considered ancestral to the ichthyosaurs.

### IV. *Order* CROCODYLIA Wagler.

We must exclude from the *Crocodylia* the *Parasuchia* of Huxley and embrace only the *Mesosuchia* and *Eusuchia* of Huxley with the addition of the typical marine forms, the *Thalattosuchia*, recently monographed by Fraas.

### V. *Superorder* DINOSAURIA Owen.

It is a mistake to raise this group to the rank of a subclass, as has been done by some authors, because its three great subdivisions certainly lead back to a common stem form in the Permian which was not dissimilar to the type represented by the *Protorosauria*.

The ordinal nomenclature still requires further study. At present I am disposed to place the carnivorous forms in the order *Theropoda* Marsh, including two suborders, (1) *Megalosauria* for the large types with solid, hour-glass shaped

vertebræ, (2) Symphypoda Cope for the smaller types with hollow, cylindrical vertebræ.

The Opisthocœlia of Owen although proposed as a 'suborder' of Crocodilia appears to enjoy priority of definition over the Cetiosauria of Seeley or the Sauropoda of Marsh.<sup>1</sup>

Similarly the Orthopoda of Cope is distinctively prior to the admirable term Predentata of Marsh. In the selection of these terms we cannot be governed by our preferences; we are bound to stand by the law of priority.

#### VI. *Superorder* SQUAMATA Oppel.

This superorder ranks in value with the Diaptosauria and Dinosauria inasmuch as it includes the very wide adaptive radiation of three groups of animals which were undoubtedly closely related in origin, namely: (1) Lacertilia, (2) Mosasauria, (3) Ophidia.

The radiation of the Mosasauria from the Lacertilia is analogous to that which we have observed occurring independently in three orders of the Diaptosauria, namely, the Proganosauria, the Choristodera, and the aquatic Rhynchocephalia of the Jurassic.

#### VII. *Order* PTEROSAURIA Kaup.

There is no question as to the Diapsidan relationships of the Pterosauria and as to their original derivation from Rhynchocephaloid types, although their specialization has carried them to a very great extreme of separation from any known Diaptosauria.

#### CONCLUSIONS.

I trust that the reclassification of the Reptilia here outlined, and the order of arrangement here adopted will be found to simplify their study. Memoirs now in preparation by Broom on the Procolophonia, by Case on the Pelycosauria, by Brown on

<sup>1</sup> Riggs, E. S. Structure and Relationships of Opisthocœlian Dinosaurs. Part I, *Apatosaurus* Marsh. *Field Columbian Museum Publ.* No. 82, Aug. 1, 1903.

the Choristodera, by McGregor on the Parasuchia, will further elucidate the still numerous and perplexing questions of phylogeny.

*Origin of Aves.*—The birds probably originated from a group of Diaptosauria identical with or closely related to that which gave rise to the Dinosauria. It is not true that birds have descended from dinosaurs, but there is very strong evidence that birds and dinosaurs are descended from a common stock.

*Origin of Mammals.*—There is no question that the mammals are affiliated with the subclass Synapsida rather than with the Diapsida; both in skull and shoulder girdle structure and in the phalangeal formula they are Synapsidan.

As to their nearer relationships they appear to be rather with the superorder Anomodontia and with the order Cynodontia or Theriodontia. The divergence of the mammal stem from these typical reptiles will probably be found to have occurred in the Permian or Lower Trias of South Africa. In fact Broom has recently described what he believes to be a mammal jaw, *Karoo mys*, from the Karoo Beds of South Africa.

AMERICAN MUSEUM OF NATURAL HISTORY,  
December 28th, 1903.



## THE EARLY DEVELOPMENT OF DESMOGNATHUS FUSCA.<sup>1</sup>

HARRIS HAWTHORNE WILDER.

IN a former number of the *American Naturalist* (March, 1899) I presented what seem to have been the only published observations on the development of one of our commonest and most generally distributed salamanders, *Desmognathus fusca*, but as I was then unable to describe the early stages, a most essential gap in this history remained unfilled.

The eggs which furnished the object of my former sketch were laid in the laboratory terrarium on or about June 1, 1898, but as the first observations were made on them June 11, at which time they were in the form of well-formed embryos coiled about enormous yolk-masses, the first eleven days of the development remained unknown, a period which includes the extremely important cleavage stages, the formation of the blastopore and the beginning of the head and tail folds.

Since that time a number of specimens of *Desmognathus* have been kept in our terrarium each spring, and the favorite hiding-places investigated daily during the egg-laying season, but with no success until the present year (1903) when on June 22 at 1.00 P. M., there was found a batch of twenty freshly laid eggs associated with a small but evidently mature female. At this time the eggs were in the early cleavage stages, and varied from the two-celled stage with the second cleavage forming to that of 16 cells, as represented by the first five rows of Fig. 1. Nine of these were preserved at once in 5% formaline, and the remainder were killed, one or two at a time at intervals representing the most important stages. The eggs were, however, rather few in number, and in spite of considerable conservatism in the daily sacrifice, there were but two left when cleavage was com-

<sup>1</sup> From the Zoological Laboratory of Smith College.

pleted and the blastopore was about to be formed. These two, compelled on June 27 to make a journey with me to Maine, in spite of the utmost care, did not survive the hardships of travel and the experiment came to an end. I am thus able to record the development only during the first three days of existence, leaving the period from the fourth to the eleventh still unknown save through analogy with allied forms, and waiting to be written when occasion may offer.

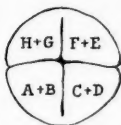
This early history includes only surface study, mainly of preserved material, but seems to be of especial importance as showing a genuine holoblastic type of cleavage when from the later form of the embryo a meroblastic form was to have been expected.

The various cleavage stages are represented in Fig. 1, in which the first perpendicular column represents them as seen from the upper pole, the second from the side, and the third from below; the figures in each horizontal row representing several views of the same egg. Of these stages the first five occurred simultaneously at the time the eggs were found, 1.00 p. m. June 22, and as no eggs were found the day before, they probably represent stages of 6-15 hours, resulting from eggs laid at intervals during the preceding night.

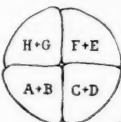
The successive changes and the descent of the various cells seem evident, and may be traced with an approximate certainty as far as the 23-cell stage, as indicated by the lettering. In the first stage shown, the first cleavage is complete, separating the egg into its two halves, A + B + C + D and E + F + G + H, while the second cleavage, beginning at the upper pole, has proceeded nearly to the equator and is separating the halves into the components A + B, C + D, E + F and G + H, a stage which is seen completed in the second row.

The third cleavage, at least in the eggs examined, is not the typical horizontal one which might be expected, but consists of a set of four meridional ones, which start near the upper pole as so many separate fissures from one of the two former cleavage planes, probably the first. Similar fissures were observed in one instance near the lower pole and it is evident that those from above and those from below meet one another, and result

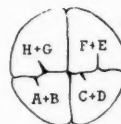
1st cleavage completed,  
2nd cleavage begun,  
June 22, 1.00 P. M.  
[The eggs were found  
at this date, and then  
presented various  
stages, from this to  
that of 16 cells.]



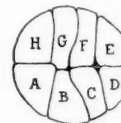
2nd cleavage completed, 4-celled stage.  
June 22, 1.00 P. M.



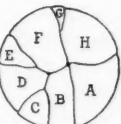
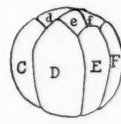
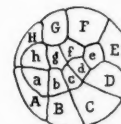
Beginning of 3rd cleavage.  
June 22, 1.00 P. M.



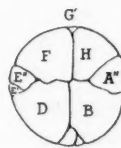
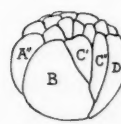
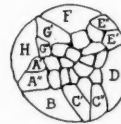
3rd cleavage completed,  
8-celled stage. June  
22, 1.00 P. M.



4th cleavage completed  
16-celled stage. June  
22, 1.00 P. M.



28-celled stage, with 16  
micromeres, 12 mac-  
romeres. June 22,  
4.30 P. M.



42-celled stage, with 36  
micromeres, 16 mac-  
romeres. June 22,  
11.00 P. M.

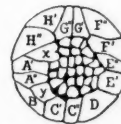


FIG. 1.—Eggs of *Desmognathus fusca* [1903 material]. Segmentation stages, observed June 22, between 1.00 and 11.00 P. M. The left-hand column shows upper poles; the next side views; and the right-hand one, lower poles.  $\times 6$ .

in the formation of an eight-cell stage, which is bilateral along the plane of the first cleavage, and consists of the four cells A. B. C. and D. upon one side, and of E. F. G. and H. on the other (fourth row of Fig. 1). These eight meridionally arranged blastomeres do not seem to have equal value in respect to size, for through a slight obliquity in these four new lines of cleavage there result four smaller blastomeres which alternate with four larger ones, and of these the latter alone usually attain the lower pole while the former ones do not reach it. This is seen by a study of the lower pole views in the fifth and sixth rows of Fig. 1, where the smaller blastomeres A. C. E. and G. intrude like wedges along the lines of the first two cleavages, but do not reach the pole save in the single instance of A. in the fifth row, an unusual condition.

The next cleavage is an horizontal one, forming an approximate circle about the upper pole, and cutting off small segments from each of the eight blastomeres of the preceding stage (fifth row). This results in a 16-cell stage, consisting of eight micromeres, a, b, c, etc., clustered about the upper pole, and eight macromeres, the remaining parts of the original cells. This last cleavage takes place so far above the equator of the egg that it does not change the aspect of the lower half, and thus the drawing of this egg (the third of the fifth row) would answer equally well for the preceding one.

By a comparison with Eycleshymer's studies of *Amblystoma*, (*Journal of Morphology*, Vol. X, 1895) it becomes evident that this latter cleavage is the one which is described as typically the third in Amphibian eggs, and that the four meridional cleavage lines which result in the formation of the 8 cell stage, together form the usual fourth. Indeed, this transposition of the two cleavages occasionally occurs in *Amblystoma*, and as my observation rests upon the study of but two eggs, it cannot be asserted that the order described is the typical one in *Desmognathus*. It is, however, identical with the method shown and figured by Kerr in *Lepidosiren*, and his figures of the third cleavage (by means of the four short lines) as copied by Ziegler (Figs. 213-314 of his *Entwicklungsges. der niederen Tiere*. 1902) would serve in every respect as better pictures of Des-



mognathus eggs in the corresponding stages than I have been able to draw. The occurrence of the third meridional before the horizontal cleavage seems also to be the rule in *Acipenser* and in *Amia*.

The next stage, that of 28 cells, is shown in the sixth row, and appears to consist, first, of a division of each micromere, increasing their number to 16, and, secondly, of a longitudinal division of the smaller macromeres A, C, E, and G, into A'. A'' C'. C'' etc., while the other four B. D. F. and H. remain undivided. The subdivisions of the smaller macromeres may or may not be visible from the lower pole, as is seen in the third figure of the row.

Beyond this the subdivisions cannot be followed with certainty, but the last figure shown (seventh row of Fig. 1) which consists of 26 micromeres and 16 macromeres, 42 in all, appears in some

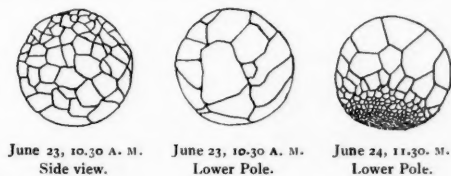


FIG. 2.—Eggs of *Desmognathus fusca* [1903 material]. Later segmentation stages, representing a direct continuation of the series shown in Fig. 1.  $\times 6$ .

respects to show some regularity, although in others it is disappointing. We would expect, indeed, to account for the increase from 12 to 16 macromeres by a subdivision of each of the remaining ones, B. D. F. and H, but while this can be seen to be the fact in the case of F and H, the two other new macromeres cannot well be explained by a subdivision of B and D. Instead of this, they appear as those marked x and y, and the relation of those and of B and D to the smaller intruded macromeres is such as not to allow the desired interpretation. Less difficulty appears in the interpretation of the 26 micromeres, for while we would naturally expect a doubling of each of the 16 of the former stage, and a consequent 32 in this, its smaller number may well be accounted for by the supposition that some of the original 16 have not yet divided. No definite interpretation

can be made, however, for this 42-cell stage, since but a single specimen was available for study, but it may be seen from the above sketch of this and the preceding stages that the eggs of *Desmognathus* will furnish a very interesting and convenient object for the study of cleavage problems in Amphibia.

Sketches of two later cleavage stages are given in Fig. 2 and may be seen to consist of a greater and greater subdivision of both micro- and macromeres, apparently without special regularity. The last figure (June 24) represents the lower pole of the oldest stage I succeeded in obtaining.

The above observations, which establish the fact that the

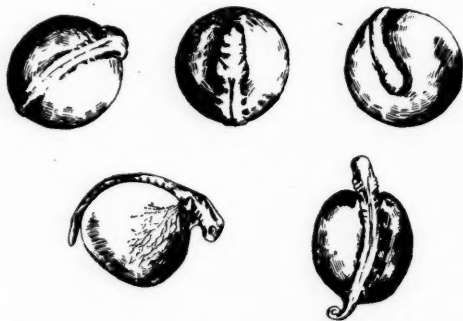


FIG. 3.—Early embryos of *Desmognathus fusca* [1898 material]. The figures in the upper row represent different aspects of a single egg of the stage described in the previous paper as "A." Similarly, the two figures of the lower row represent different aspects of the stage described primarily as "B."  $\times 6$ .

eggs of *Desmognathus* are holoblastic, will serve to correct the statement to the opposite effect given in my previous article on the subject, and while it is always unpleasant to be proven in a mis-statement, it is more satisfactory to the investigator to be able to furnish his own proof than to leave it to others. At the time of writing my previous article, I possessed no embryos younger than those represented in the upper row of Fig. 3, and it then appeared to me impossible that such a relation between embryo and yolk as the one shown here could result from an egg of the holoblastic type. A slightly older stage, that represented in the second row of Fig. 3, seemed still more convincing in this respect, since by this time a set of branching blood vessels

had made their appearance on the surface of the yolk, reminding one forcibly of similar embryos *e. g.*, those of certain Teleosts, that result from meroblastic eggs. Too sharp a distinction between the holoblastic and meroblastic type cannot, however, be drawn, since there are numerous transition forms, as that of *Salamandra maculosa*, in which the egg is 4-5 mm. in diameter, and the first two cleavage planes, although they slowly cut their way around the egg on the outside, often fail to divide the yolk internally, "so dass die Furchung in den ersten Stadien partiell ist" (Ziegler *loc. cit.*, p. 249, on the authority of Grönroos, 1903). A similar condition has been produced experimentally in the frog's egg by O. Hertwig (1897). The eggs of the Gymnophiona, which are the largest of all Amphibian eggs, (7-8 mm. in *Hypogeophis rostratus*) are at first typically meroblastic, with a germinal disk that spreads gradually over the yolk; but during and after gastrulation the yolk becomes divided up into large cells, so that the eggs are ultimately holoblastic.

In these latter, also, as well as in the eggs of *Salamandra* and *Desmognathus*, there is a noticeable array of blood vessels upon the yolk, which at first sight closely resembles a true yolk circulation, but which in reality consists of the vessels which normally appear superficially in the region distended by the yolk mass, and thus, although they may receive nutriment from the yolk, they are in no sense true vitelline vessels. The veins of this region, though not the arteries, could be closely followed in the two series from which Figs. 4 and 5 were taken, and are shown to be three in number, one median and two lateral. The median vein lies along the mid-ventral line of the swollen abdomen, scarcely noticeable posteriorly, but increasing anteriorly as it picks up several lateral branches. It passes along the dorsal (concave) aspect of the liver and enters the sinus venosus in company with the hepatic vein. By its position and course it undoubtedly corresponds to the abdominal vein of the adult, and thus, although it may be also a potential portal, it cannot be very definitely related to the true vitelline veins of meroblastic embryos. In the same way the two lateral veins are seen to be identical with the large cutaneous veins which lie along the sides

of the trunk. They empty into the *Ductus cuvieri* near the entrance of the subclavian.

Thus, although it is seen that many Amphibian eggs are on the border between the holoblastic and meroblastic types, and although they form interesting transitions between the two, especially useful in breaking down artificial distinctions, yet it must be confessed that through the observations here recorded the eggs of *Desmognathus* are at first almost typically holoblastic, although in the later relation of embryo to yolk they greatly resemble meroblastic embryos. (cf. Fig. 3 of this paper with the following in Ziegler's text-book, 1902, Fig. 304.) Hypogeophis (Brauer); Fig. 188 herring (Kupffer).

In concluding this paper I wish to present a few sections

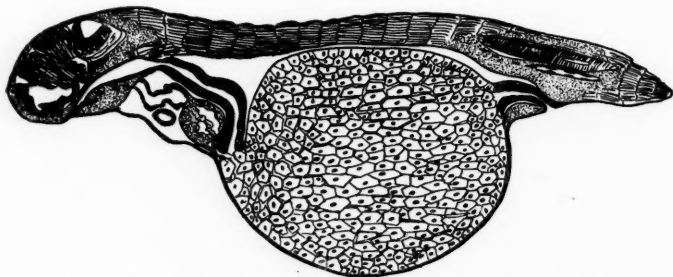


FIG. 4.—Sagittal section, a little to one side of the median line, of an advanced embryo of *Desmognathus fusca* [1898 material] a little older than "Stage D" of the previous paper.  $\times 15$ .

taken through advanced embryos of *Desmognathus* (the 1898 material) which will show the actual relation of the embryo to the large yolk mass and will demonstrate its cellular character in the later stages.

Fig. 4 is a sagittal section of an advanced embryo, and shows the median relationships in the ventral half, but strikes the brain and the dorsal portion somewhat laterally. By combining several adjacent sections, the pharynx, oesophagus and anus were completed. In this the peritoneum may be followed dorsally as a continuous line investing the rectum, the yolk mass and the oesophagus, and enclosing a portion of the coelom; and ventrally around the yolk mass enclosing a large coelomic space

ventral to heart and liver and a smaller one ventral to the anus. The entire yolk mass, which is wholly cellular, is enclosed within the peritoneum and is morphologically the equivalent of the middle portion of the intestinal tract in which a lumen has not as yet appeared. Fig. 5 shows four cross-sections of an embryo a little older than that of Fig. 4 and taken from a single series, the first through the liver, the second through the yolk at its greatest circumference, the third through the hip-girdle and rectum and the fourth through the cloaca, with the hind-limbs at the side. The numbers attached to each are those of the sections as numbered in the series. These show the same relationships as seen in Fig. 4, the second especially, in which two lateral

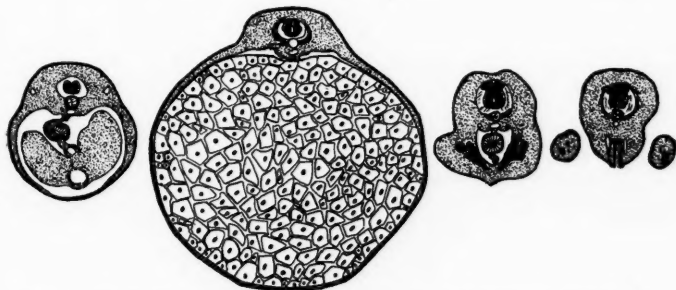


FIG. 5.—Four cross-sections from an advanced embryo of *Desmognathus fusca* [1898 material] slightly older than Fig. 4. The sections are 20  $\mu$  in thickness, and the complete series, from the tip of the nose to the end of the cloaca consists of 335 sections. The numbers affixed to the sections in the figure indicate their place in the series.  $\times 15$ .

coelomic spaces may be seen dorsal to the yolk-mass, separated by a mesentery. In the first the alimentary canal (oesophagus or beginning of stomach) is suspended between dorsal and ventral mesenteries, in the latter of which lies the already well-developed liver, while in the former is seen the beginning of a pancreas. In the third section are seen the two lateral coelomic cavities, dorsal and ventral mesenteries, the hip girdles and the heads of the femora, and in the fourth are the last (most posterior) remnants of the coeloms, the open cloaca, and the two legs, the one cut through the femur, and the other through tibia and fibula.

SMITH COLLEGE,  
Nov., 1903.



## THE HISTOLOGY OF THE LIGHT ORGANS OF *PHOTINUS MARGINELLUS*.<sup>1</sup>

ANNE B. TOWNSEND.

ORGANIC light has always been a subject of interest, both to the scientist and to the casual observer of nature, and no other photogenic organisms are of such wide range and easy access as the fireflies. In some of its phases the light of the firefly comes within the scope of the physicist and chemist. To the former belongs the consideration of its nature, of its spectrum and other physical properties; to the latter come the problems of chemical analysis concerned with the phenomenon, but to the student of entomology remains the study of the delicate living structure in which this wonderful process of photogeny takes place.

In spite of the abundance of these insects, little work has been done on the structure of the light-organs in our American fireflies. During the past twenty years some careful investigations have been made upon European and Cuban forms, but there is practically no literature upon those of our own country. The purpose of my study has been to learn something of the histology of the light-organs of *Photinus marginellus*, the most common firefly about Ithaca during June and July. This work was begun at the suggestion of Dr. Wm. H. Seaman of Washington, D. C., whose advice during its progress has been most helpful. I am also indebted to Professor Comstock and to the members of his staff at Cornell University for their kindly supervision of my work.

The material from which this work was done was collected near Cornell University during the summers of 1901 and 1902. The insects begin to appear by the middle of June, but are not abundant until July. The height of the flying season is during the first part of July. The large majority of the insects

<sup>1</sup> Contribution from the Entomological Laboratory of Cornell University.

caught were males. A number of females were found, but never on the wing. They were always either in the grass, or on some low plant where they could easily have climbed.

Three methods of fixation were tried the first summer. For two of these the insects were killed by dropping into hot water. The caudal part of the abdomen was then clipped off and put into the fixing fluid without removing any part of the chitin. Half of this material was fixed for twenty-four hours in Flemming's solution (strong). This proved almost worthless, with the exception of a single slide. The other half of this material was fixed in Gilson's mercurio-nitric solution for seven hours. This gave very good preparations of the general features of both layers of the light-organs.

The third lot of material was killed and fixed in hot 70% alcohol. This was satisfactory for the gross structure of the organs, though not good for the finer details.

The second summer the killing of the insects in hot water was abandoned. The caudal portion of the abdomen was clipped off, the tip cut away, and the dorsal wall removed to insure better penetration of the fixing fluid. The living tissue was then put directly into the fixer. Flemming's fluid, after this treatment, gave much better results than before. Hermann's fluid gave a fairly good fixation. The cells of the cylinders are definitely outlined in these preparations, but the tissues in general are opaque.

By far the best results for the tracheal structures were obtained by the use of osmic acid. The strength of the acid was varied from .1% to 1%, and the time of fixation, from two to thirty hours. The best preparations were from material left for thirty hours in 1% osmic acid.

Material fixed in Flemming's or Hermann's fluid, or in osmic acid, was washed for twenty-four hours in running water. That fixed in Gilson's fluid was put directly into 70% alcohol. All the material was dehydrated by carrying it through the grades of alcohol, from 70% to absolute. Cedar oil was used for clearing. These sections were all cut in paraffin.

The greater part of the sections were cut 10  $\mu$  in thickness, but a few thinner sections, 3  $\mu$  and 5  $\mu$ , were made for the determination of some finer structural points.



The material was all stained after the sections were cut. The Gilson and alcoholic sections were stained for about two minutes in Gage's chloral hematoxylin, and for a half minute in eosin. This gave satisfactory general results. A double stain with alum carmine and picric acid did not prove a good stain after Gilson's fluid. Following fixation with osmic acid, Hermann's or Flemming's fluids, safranin proved most satisfactory. The sections were stained for twenty-four hours in a mixture of equal parts of saturated aqueous and alcoholic solutions of safranin, then differentiated in absolute or even slightly acid alcohol. Iron hematoxylin is also a good stain for osmic acid material.

Carbol-xylene was used as a clearer, and the sections were mounted in Canada balsam.

Teazed preparations were made by dissecting out the light-organs entire, placing them for from fifteen to thirty minutes in .5% osmic acid, then for a few minutes in weak caustic potash, and teasing in normal salt solution.

Experiments with methylene blue injection were not successful. Only one insect showed any coloration of the central nervous system, and in that the finer nerves could not be traced. It is difficult to get a good injection with such small insects. However, my attempts in this line were begun near the close of the collecting season, and with further experimenting it is possible the results might have been better. The most successful specimen was killed an hour and a half after injection.

Since the old idea that the firefly's light was dependent upon the presence of phosphorus or some similar substance has been abandoned, other theories have been advanced in attempt to explain the phenomenon. The view generally accepted is that the light results from the oxidation of a substance produced by the metabolism of the light-organ cells. The nature of this substance has not been determined, but that its photogenic property is independent of the life of the cell is proved by the fact that when the organs are dried and reduced to a powder the light reappears under the influence of air and moisture. When the fresh photogenic tissue is crushed, the light increases in brilliancy, and it is some time before it wholly disappears. Radziszewski ('80) through his study of the artificial luminosity

of lophin, discovered a series of carbon compounds similar to those found in living organisms and capable of becoming luminous under conditions compatible with life. The conditions necessary for this production of light he found to be the presence of oxygen, an alkaline reaction and slow chemical action. Watasé ('96) states that in the firefly the phenomenon is due to the oxidation, in alkaline media, of a granular substance secreted by the cells of the photogenic tissue. He offers no further suggestion as to the character of the substance than that it is "a secretion of fatty nature." He gives as proof of the oxidation theory the fact that when the photogenic material is crushed on a slide and lowered into a jar of carbon dioxide the light disappears instantly, but reappears when the slide is placed in a jar of oxygen, or simply in the air. This may be repeated several times with the same material. Watasé recognizes the necessity of moisture as well as of oxygen in the process of photogeny.

Dubois stands almost alone in opposing the theory of oxidation. As a result of experiments with ozone, nascent oxygen and oxygenated water he states ('95), that the action of energetic oxidizing reagents at once and finally extinguishes the light, without first causing any increase in brilliancy. However, the absence of oxygen seems to destroy the light, as it is suspended when the light-organs are placed in a vacuum. From his earlier work he concluded that the light was the result of a process of crystallization. His later work ('98\*) has led him to abandon this theory. He still rejects the oxidation hypothesis as crude and unscientific, and offers in its place one of a reaction between two substances to which he has given the names luciferase and luciferine. The accessibility of the material led him to use *Pholas dactylus*, a marine mollusk, as the basis of his study. The inner wall of the siphon of a large *Pholas* was scraped with a knife and the resulting pulp crushed with sand and 95% alcohol. After twelve hours it was filtered and a liquid obtained which was not luminous, even after vigorous agitation with air. The alcohol was drained off from the residue and chloroform added. After some hours a second non-luminous liquid was filtered off. A mixture of one part of the first liquid with three parts of the second gave a beautiful

luminescence at ordinary temperature. By adding to liquid No. 2 five or six times its volume of 95% alcohol, or by boiling it, a white floccose precipitate was formed and the mixture of the remaining liquid with liquid No. 1 no longer produced light. He therefore considers the white precipitate as constituting one of the two photogenic substances, the luciferase. Luciferine was obtained in an impure state by evaporation of alcoholic liquid No. 1. Another experiment was tried with the luminous mucous secreted by *Pholas*. Two portions of the mucous mixed with water were taken, and one extinguished by agitation, the other by bringing to the boiling point. The mixture of the resulting non-luminous liquids was photogenic. A similar result was obtained with the prothoracic organs of *Pyrophorus noctilucus*. One was extinguished by crushing, the other by dropping it into boiling water. When the latter was crushed and mixed with the former, the light reappeared.

Dubois therefore states that he has established experimentally that the light of living organisms is produced, in the presence of water and oxygen, by the reaction between luciferase, an instable proteid substance possessing in large measure the general properties of an enzyme, and luciferine, a chemical substance. While Dubois confidently asserts that biological light is not a result of oxidation, his experiments would not seem to prove this conclusively. He himself admits the necessity of oxygen, and even if the process is not one of simple, complete oxidation, it would yet seem probable that oxidation is the essential factor in photogeny.

The photogenic tissue of *Photinus* responds definitely to the action of oxygen. A series of experiments shows uniformly a decided increase in the brilliancy of the light when the tissue is placed in a jar of oxygen. Tissue in which the light has been wholly extinguished by the action of carbon dioxide becomes instantly photogenic when placed in oxygen. Until there has been more extensive experimental study of a large number of organisms, generalizations on the subject of organic light are unsafe.

The fact that Dubois's work was done upon a marine organism is significant. If, as one must assume, the photogenic function

has arisen independently in different organisms, it would not seem strange that the light of such widely separated forms as a marine mollusk and a terrestrial insect, though in both cases a process of oxidation, might be produced in a different manner.

The physical properties of the firefly's light have been studied by Dubois, Langley and Very, Young, and Watasé, with essentially the same results. The spectrum given by the light of the Lampyridæ is perfectly continuous, without any trace of lines, either bright or dark. It lies within that portion of the spectrum which most powerfully affects the organs of vision, though having small thermal or actinic effect. Dubois has demonstrated by photography the presence of some actinic rays in the light of *Pyrophorus*. A single insect was used, and five minutes was required for printing from a plate which would have taken only a fraction of a second with sunlight. Dubois attributed the presence of actinic rays to a fluorescent substance which he found in the blood.

Most careful and elaborate experiments have failed to show more than an infinitesimal amount of heat connected with the light. One authority even goes so far as to say that not more than one-thousandth of the energy expended in the flash of the firefly is converted into heat waves. When one considers that in our ordinary oil or gas lamps more than ninety-nine per cent of the energy is lost as regards illumination, and that even in the arc light only about ten per cent. of the waves are visible, the interest which this "cheapest form of light" arouses from the economic point of view is very apparent. It is also an alluring problem to the student of physics to determine by what process the medium wave lengths are produced independent of the longer and shorter waves. If this "secret process" could be wrested from nature, its economic value would prove almost inestimable.

While the phenomena of biological light early attracted the attention of observers of nature, as Aristotle, Democritus and the naturalist Pliny, it is only within the last century that any serious study has been given to the organs which produce it. The discovery of their cellular nature may be credited to Peters. In 1841 he refuted the theory of Carrara ('36) that the light was dependent upon an air-sac extending from the mouth to the light-

organs and acting as a bellows, and stated that the photogenic tissue was made up of little spheres, regularly arranged and penetrated by the tracheæ. Leydig and Kölliker in 1857 definitely recognized the cellular structure of the light-organs. Their work has been followed by that of several other European investigators. During the past twenty years Wielowiejski and Emery have made important histological researches upon species of *Lampyrus* and *Luciola*.

All recent workers agree in stating that the ventral light-plates of the male lampyrids are composed of two more or less clearly defined layers; the dorsal, chalky, opaque layer, and the ventral, or truly photogenic layer. The former is composed of fairly regular, polygonal cells, filled with a great quantity of crystals of urate salts. The ventral layer is composed of two distinct elements; the tracheal structures and intermediate areas of parenchyma. The parenchyma cells contain fine granules of non-urate composition. The main tracheæ of the photogenic segments send vertical branches down through the light-organs. Aside from their profuse branching they show no unusual features until they reach the ventral layer. The tracheal structures within the ventral layer differ in different forms, and the two species upon which Wielowiejski and Emery based the bulk of their work, *Lampyrus splendidula* and *Luciola italica* respectively, show a considerable difference in this respect. In *Luciola* each vertical tracheal axis is surrounded by a cylindrical mass of semi-transparent tissue, within which it branches in an arborescent manner. The method of branching in *Lampyrus* is fasciculate, rather than aborescent, and the tracheæ are much less regular in their distribution. Max Schultze, in 1864, found in osmic acid preparations from the light-organs of *Lampyrus splendidula* certain blackened bodies at the periphery of the cylinder. These he found to be penetrated by the finer tracheæ. Failing to find further continuations of the tracheæ beyond these bodies, he called them the "tracheal end cells." Wielowiejski ('82), in his study of the same species, found that instead of having their ultimate endings within the so-called "end cells," the tracheæ branch, sending out fine "tracheal capillaries" which extend beyond the cylinder and in most cases anastomose with those of

adjoining cylinders. Emery, from his work on *Luciola*, confirms the views of Wielowiejski in all points except as regards the anastomosing of the capillaries. He found them always ending free, never uniting with those from the same or another cylinder.

In this work the nomenclature previously used has been retained except in a few cases where a change seemed especially advisable. The more familiar terms phosphorescent and luminescent, with their nouns, are abandoned and photogenic and photogeny substituted. Phosphorescent is objectionable as it suggests that the light is due to the presence of phosphorus. Photogenic — light-generating — gives a more definite idea of the actual phenomenon than luminescent. The name "end cells" was used by Max Schultze because he believed the tracheæ had their ultimate endings within these cells. Now that it is proved that the tracheæ do not so end, but merely pass over into the tracheolar network, the name "transition cells," as used by Holmgren ('96), is far preferable. The term tracheoles, which is used elsewhere in insect histology to designate fine tracheal branches not possessing spiral thickening, is preferable to "tracheal capillaries."

The light-organs of the male of *Photinus marginellus* are in the form of two plates lying above the ventral body wall of the

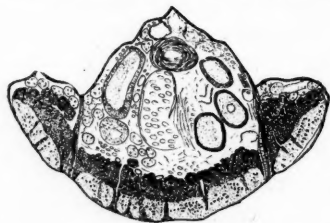


FIG. 1.—Transverse section through entire abdomen.  $\times 20$ .

fifth and sixth abdominal segments. (Figs. 1 and 2.) The underlying cuticle is transparent, allowing free emission of the light. The plates lie just beneath the central nervous system and directly upon the very thin hypodermis. They are yellowish white in color. In the female of the

same species there is only a single, somewhat spherical organ in the centre of the fifth segment. In this work all descriptions of structure refer to the light-organs of the adult male. The main tracheæ of the photogenic segments send branches ventrad through the light-organs. Thus the dorsal surface in fresh

material is shown to be penetrated by numerous tracheæ. The vertical or oblique tracheæ continue to branch profusely in an arborescent manner. This repeated branching is characteristic of the tracheæ of the photogenic tissues. The tracheal epithelium is composed of thin, flattened cells, with large flattened nuclei. Prominent hair-like projections of the intima are abundant in the lumen of the large tubes. These internal chitinous hairs have been noted in *Lampyris* by Gerstæcker, and in *Luciola* by Emery. The light-organs are innervated by nerves from the last two abdominal ganglia. These ganglia are both situated in the fifth segment, over the more cephalic light-plate. I failed to trace more than these primary nerve branches, as my attempts at methylene blue injection were unsuccessful.

Each light-plate is composed of two distinct layers, in this



FIG. 2.—Longitudinal section through abdomen from fifth segment to caudal end.  $\times 20$ .

respect agreeing in structure with the European species which have been studied. In none of my preparations have I been able to detect any trace of a membrane, either surrounding the light-organs or separating the two layers. Wielowiejski ('82) states that in *Lampyris splendidula* each light-plate is surrounded by a delicate film of connective tissue, in which small rounded nuclei may be faintly seen in well stained material. He gives no figures of this, however. Emery ('84) says there is no indication of a membrane in *Luciola*. The two layers cannot be distinguished in fresh material, but a difference in the two surfaces of the light-organ is apparent. The dorsal surface is a bright chalky white, while the ventral surface appears yellowish and luminous. Examined with a low power of the micro-



scope the dorsal surface is seen to be divided into polygonal areas.

The appearance of the cells of the dorsal layer varies much with the treatment of the tissue. Material fixed in alcohol and brought in contact with water for but a short time in staining with hematoxylin shows the cells filled with a dense content of coarse granules. With reflected light these granules still show their characteristic chalky whiteness, while with transmitted light they are brown. Granules identical in appearance are also found in the fat cells of the same region of the body. Material fixed in any fluid requiring subsequent washing in water shows

a considerable decrease in the granules of the dorsal layer.

This verifies the statement of Wielowiejski that these granules are insoluble in alcohol, but soluble in water. Kölliker, in 1857, proved them to be crystals of urate salts, and his results have been accepted by Wielowiejski and Emery. When the crystals have been dissolved out the form of the cells is easily determined.

They are polygonal, fairly regular in outline and simi-

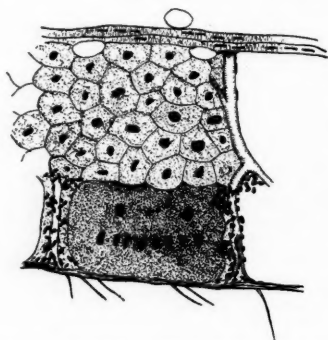


FIG. 3.—General features of both layers of light organ. Gilson's fluid, hematoxylin and eosin.  $\times 75$ .

lar in size. They average about  $28\ \mu$  by  $25\ \mu$ . Those upon the upper surface are somewhat more spherical than those beneath. Large nuclei are always present, but the cytoplasm seems to have been almost entirely replaced by the granular secretion. (Fig. 3.)

The dorsal layer not only forms a plate resting upon the ventral layer, but it projects beyond the latter and extends along its caudal surface to the body wall (Fig. 2). There are two groups of muscle fibres in each light plate, extending from the dorsal to the ventral body wall in the lateral portions of the plate. These muscles are surrounded by a layer of cells distinctly separated from the cells of the ventral layer and contin-



uous with those of the dorsal layer. In material in which the dark granules of the dorsal layer cells have not been dissolved out, they are found equally in the cells surrounding these groups of muscle. (Fig. 1.)

The ventral layer is composed of two distinct elements, the so-called parenchyma cells, and the cylinders. The cells of the parenchyma differ from those of the dorsal layer in being very irregular in shape and size. Occasional cells extend from the dorsal surface of the layer to the body wall.

In some cases the depth is several times the thickness, while some cells are almost spherical. In some places the ventral layer is found to be several cells deep. (Fig. 4.) The size of the cells varies considerably. The granular secretion in these cells is much finer than that in the dorsal layer. Max Schultze has stated that these granules are of non-urate composition. He examined the granules of both layers with polarized light, finding that those from the dorsal layer were bi-refractive, but that those from the ventral layer were



FIG. 4.—Cells of parenchyma. .3 % osmic acid.  $\times 250$ .

not. Those of the dorsal layer having been proved by Kölliker to be of urate composition, he concluded the granules of the ventral layer were non-urate. Wielowiejski verified the results of these experiments, but did not agree with Max Schultze's conclusions. He states that these experiments merely prove the granules of the ventral layer to be in general amorphous. He thought, however, that the difference in composition could be readily demonstrated by reagents. He found the granules of the dorsal layer to be soluble in water but insoluble in alcohol, while the opposite was true of those of the ventral layer. Emery says that the granules of the ventral layer are not crystalline, and that they disappear altogether in balsam preparations. The cells of the ventral layer appear to have more or less of granular content in all of my preparations, including those from material fixed in alcohol. It is only in osmic acid material that cells are found comparatively free from such secretion. As all my sections are mounted in balsam, this medium would not seem

to have any decided effect. This question, however, can be satisfactorily settled only by the study of fresh tissue.

Between the areas of parenchyma are sharply defined, more or less cylindrical masses of tissue surrounding the vertical tracheal stems and their branches. It is about these cylinders and their tracheæ that the greatest interest is centered. The cylinders are from  $23\ \mu$  to  $68\ \mu$  apart, and average about  $30\ \mu$  in diameter. Their appearance differs greatly with the fixation. In material fixed in alcohol or Gilson's fluid, and stained with hematoxylin and eosin they appear as areas less granular, and consequently less deeply stained, than the intervening parenchyma. They contain a large number of small nuclei, especially abundant near the tracheæ. After fixation in Hermann's fluid and staining with safranin the cell outlines appear very distinct. (Figs. 10 and 11.) Preparations fixed in Flemming's solution and stained with safranin also show cellular structure, though not so definitely as the preceding. Less indication of the structure of the cylinders is shown in the osmic acid material.

If fresh material, placed for fifteen minutes in .5 % osmic acid and then treated for a few minutes with weak caustic potash, is viewed from the ventral surface, the cylinders appear as very distinct rings. In all preparations, both temporary and permanent, the boundaries of the cylinders are sharply defined.

Within each cylinder is a main tracheal stem which gives rise to numerous branches in the characteristic aborescent manner. There is no change in the structure of the tracheæ until near the periphery of the cylinder, where each fine tracheal twig breaks up into tracheoles. The number of tracheoles arising from one tracheal twig seems to vary somewhat. Ordinarily there appear to be only two, but three or four are not uncommon. Emery gives the number of tracheoles in *Luciola* as being uniformly two. In *Lampyrus*, Wielowiejski found the number variable, as many as six sometimes occurring.

The tracheoles are fine tracheal branches and are characterized by having no spiral thickening of the intima. Their chitinous structure is plainly shown by the fact that they persist in material treated for some time with caustic potash.

Max Schultze, Targioni-Tozzetti ('70) and Emery were all of

the opinion that the tracheoles do not contain air, but a colorless fluid. Wielowiejski also found them filled with a fluid, but recognizing the extreme improbability of such condition existing in life, he looked for some explanation of it. In dried, air-filled material mounted in weak glycerine the tracheoles as well as the larger tracheal tubes were filled with air. After about five minutes the silvery, glistening lines of air became broken up,

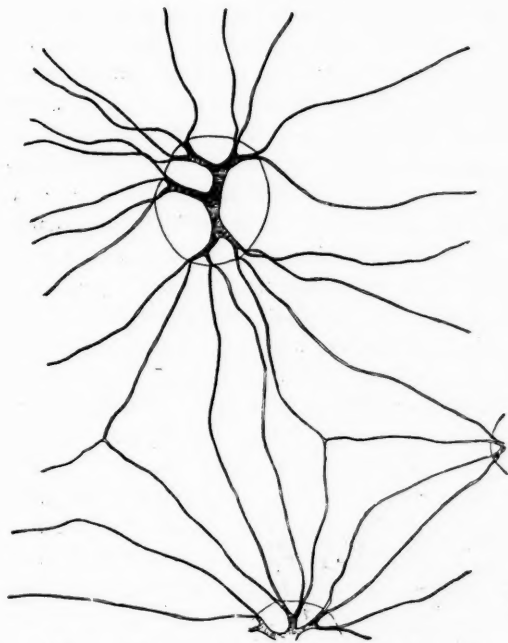


FIG. 5.—Teased preparation, showing anastomosing of tracheoles.

and gradually, from the tracheoles in, the tracheæ became filled with a fluid. This would seem to prove, what one must believe *a priori*, that the entire tracheal system is filled with air. My observations agree with Wielowiejski's, for although in my preparations the tracheoles were always already filled with liquid, the penetration of the liquid into the larger branches was unmistakably from the tracheoles in. It may be noted in this con-

nection that in the tracheoles of developing wings, structures entirely similar to those of the light-organs, the presence of air may be readily seen.

In sections parallel to the axis of the cylinder the tracheoles are generally cut, so that their entire length cannot be followed. The fact that they appear to end free cannot, therefore, be taken as any proof. In rare cases they are seen to anastomose with those of adjacent cylinders, and in sections transverse to the cylinders, beautiful demonstrations of anastomosing may be seen. If a light-organ from a freshly killed insect is placed for a half hour in .5 osmic acid, then for a few minutes in caustic potash, and then placed under the microscope, ventral side up, the tracheoles can be easily seen. The cylinders stand out as definite circular or oval rings, and from the inclosed tracheæ radiate the tracheoles. As the distribution of the cylinders is fairly regular, the network of tracheoles has a notably uniform pattern. Tracheoles from three cylinders unite at a point about equidistant from their respective cylinders. (Fig. 5.) In preparations from material fixed in Flemming's, or Gilson's fluid, the same tracheolar network may be clearly seen. (Fig. 6.)

When the ventral surface of a fresh light-organ is studied under the microscope in a dark room the light is found univer-

sally distributed throughout the parenchymatous area. The cylinders stand out as non-photogenic spots on the background of light. This shows that the photogeny occurs in that portion of the tissue where the tracheolar network is found, and where there is consequently the most abundant supply of oxygen.

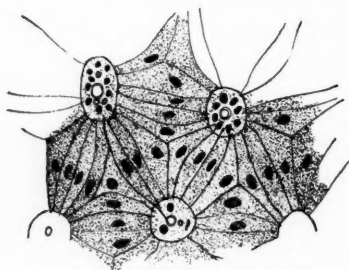


FIG. 6.—Anastomosing of tracheoles. Fleming's fluid, safranin.  $\times 150$ .

Wielowiejski found anastomosing of the tracheoles generally true in *Lampyrus*, although he admits of some exceptions to the rule. Wistinghausen and Holmgren found anastomosing of the tracheoles in the silk-glands of the caterpillar. Emery states

that in *Luciola* the tracheoles in all cases end free. This is shown in his figures 4 and 7, Plate XIX.

In *Lampyris* Wielowiejski figures the tracheoles as winding irregularly and twisted and looped about each other. In *Photinus* they are generally almost straight. They may be slightly wound about each other, but for the most part they pass directly from one cylinder to another.

Both Wielowiejski and Emery agree in considering that the tracheoles pass between the cells of the parenchyma, although positive proof is difficult. In no case has any portion of a tracheole been found within the parenchyma cells, although they have been seen closely applied to the exterior of the cells. In surface sections of *Photinus* the areas between the tracheoles would appear to correspond to cells, each possessing a nucleus. It thus seems altogether probable that in their course outside the cylinders the tracheoles are intercellular.

In 1864 Max Schultze studied the light organs of *Lampyris splendidula*, using osmic acid as a fixer. He found the finer tracheal branches losing their spiral thickening and passing into star-shaped, finely granular bodies which he believed to be true cells possessing distinct nuclei and cell membranes. He failed to find any continuation of the tracheæ beyond these stellate cells, and so assumed that these cells enclosed the ultimate endings of the tracheæ. The name "tracheal end-cells," as given by Max Schultze has since been generally used, even by those who knew it to be a misnomer.

In his studies of the same species, Wielowiejski found the tracheæ passing into the stellate "end-cells" of Max Schultze, but instead of ending there, branching to form tracheoles which penetrate the inter-cylindrical parenchyma. He believed these "end-cells" to be true cells, much flattened and similar in form to the endothelial cells of vertebrates. They extend about the bases of the tracheoles in a web-like manner and are more or less stellate in shape. These cells show a characteristic reaction with osmic acid, causing a precipitate to be formed, especially about the point of origin of the tracheoles. The tracheal twig appears constricted at its apex, and is intensely blackened by the osmic acid. The effect of the acid varies, in some cases the entire end cell being uniformly blackened.

In the female of *Lampyrus noctiluca* and the female and larva of *Lampyrus splendidula* Wielowiejski found a somewhat different condition than in the adult male of *L. splendidula*. The tracheoles arising from the ends of the finer tracheæ are generally only two in number. They may also occur along the course of the smaller tracheæ, instead of only at the ends, and they may even arise from some of the larger tracheal branches. It is obvious that under such conditions "end-cells" like those figured for *L. splendidula* would not be present. He states, however, that there is a membrane spread out between the tracheoles, although it fails to give the characteristic "end-cell" reduction with osmic acid. From the larva of *L. noctiluca* he figures one of the larger tracheæ with its branches, with a strongly developed, nucleated membrane surrounding it much as a cylinder surrounds the tracheal axis in the imago of Photinus. The epithelium of the large primary trunks of the tracheæ in the larva shows the power of precipitating osmic acid.

Wielowiejski also studied tracheal endings in other parts of the adult *L. splendidula*. In the fat body and reproductive organs he found "end-cells" in abundance, similar to the typical ones of the light-organs in their reaction with osmic acid, but differing considerably in shape and in the number of tracheoles contained. In all these instances Wielowiejski interprets the "end-cells" as being a special development of the epithelium of the trachea. In his figures the tracheæ, before entering the photogenic tissue, show well developed epithelium, this layer being sometimes almost as thick as the diameter of the tube.

Wielowiejski neither figures nor describes cylinders in the light-organs of *Lampyrus*. After his study of *Luciola italica* ('86) he states that he found no such regular arrangement of the tracheæ here as occurs in the two species of *Lampyrus* formerly studied. He did not consider the mass of the cylinders in *Luciola* as homologous with the "end-cells" of *Lampyrus*.

In *Luciola italica* Emery found the ventral layer composed of cylinders and intermediate areas of parenchyma much as has been already described for Photinus. In osmic acid preparations he saw, just within the periphery of the cylinder, small, irregular, three-cornered masses, in which the distal ends of the tracheæ

and bases of the tracheoles appeared to be imbedded. When a tracheal axis was isolated these small bodies looked like "grapes on a stem," while from each "grape" two tracheoles proceeded. As these browned bodies were found only in the osmic acid preparations he believed them to be artifacts, and not the "tracheal end-cells" of Max Schultze. He concluded that the clear cell elements of the cylinder are the real "end-cells." Within these the tracheæ undergo their final division, each giving rise to two tracheoles. In *Luciola* only that part of the cell which is in direct contact with the bases of the tracheoles is blackened by osmic acid.

Emery agrees with Wielowiejski in considering that the "end-cells" are formed from the tracheal epithelium.

Two of the latest investigators of tracheal endings, Wistinghausen and Holmgren, have both worked on the silk-glands of lepidopterous larvæ. Both found the finer tracheæ passing over into what they term the "tracheal capillary end-network," a network formed by the anastomosing of the tracheoles and their branches. They agree in stating that the epithelium of the tracheoles is extended in a web-like manner to form the "end-cells." Holmgren discards the term "end-cells," substituting for it the more correct name of "transition cells," as these structures form the transition between the tracheal tubes proper and the tracheolar net-work.

In the light-organs of *Photinus*, fixed for thirty hours in .1 % osmic acid and stained with safranin, the transition cells may be seen most plainly. They show with varying

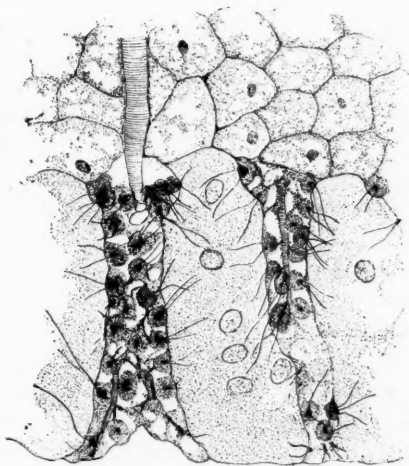


FIG. 7.—Transition cells in typical osmic acid preparation.  $\times 250$ .

clearness in all the osmic acid material, and in one insect fixed in Flemming's fluid. In the typical osmic acid preparation they appear as irregularly spherical bodies, blackened throughout but most intensely so at the point of origin of the tracheoles. They show no appearance of nuclei, but as the nuclei of the adjacent cells show only faintly with this treatment, this is not significant.

The transition cells of *Photinus* as shown in osmic acid preparations are more similar to the blackened, grape-like bodies described by Emery, than to the stellate, endothelioid cells figured by Wielowiejski. They occur at the apices of the finer

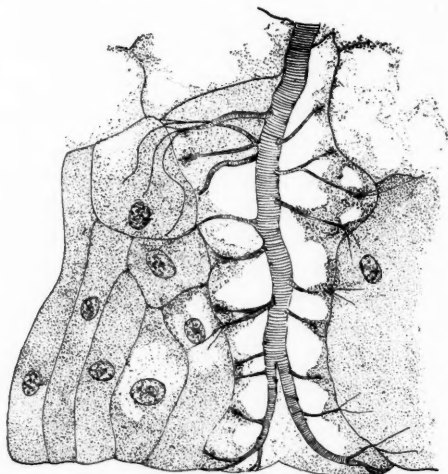


FIG. 8.—Transition cells where effect of osmic acid has been less pronounced.  $\times 300$ .

tracheal twigs, and near the periphery of the cylinder. The space between them and the tracheal axis, and the spaces between the transition cells themselves appear clear. The edges of the spheroid masses are generally irregular, and their whole appearance suggests an artificial condition. (Fig. 7.) In sections where the effect of the osmic acid has not been as extensive, the same blackening at the points of tracheolar origin may be seen, but instead of finding spherical bodies surrounding these points of furcation, the granular mass of the cylinder appears in different condition. It extends along the periphery of the



cylinder, and follows the course of each tracheal branch, in some cases almost to the main stem, so that instead of a structure resembling a cluster of grapes, one finds along the wall of the cylinder a series of fan-shaped masses, one for each tracheal twig, their apices toward the axis of the cylinder. (Fig. 8.) As there is great irregularity in the form of these dark bodies within the cylinder, and also in the shape of the intervening clear spaces, it would seem that Emery is correct in considering them an artifact.

Definite cellular structure can be seen only in the material fixed in Hermann's and Flemming's fluids. In these preparations, as in those from osmic acid, the tissue seems to be shrunken and distorted. To a large extent the nuclei appear to have been separated from the cytoplasm, and to lie in the spaces left by the shrinkage of the cells. The cells show a tendency to shrink away from each other, and away from the main axis of the trachea, thus becoming smaller, denser bodies surrounding the distal ends of the tracheal branches, and in contact with the periphery of the cylinder. (Figs. 9 & 10.)

In material fixed in alcohol or Gilson's fluid there is no appearance of cells within the cylinder, although an abundance of small nuclei may be clearly seen.

Emery suggests that the cylinder, in *Luciola*, may be a syncytium, but in both longitudinal and transverse sections of the cylinders in material of *Photinus* fixed in Hermann's fluid, the cells are clearly demonstrated.

The "end-cells" of *Lampyris* and the cylinders of *Luciola* are stated to be a special development of the tracheal epithelium. This is not true of the cylinders in *Photinus*, as the epithelium can be definitely seen, not only in the tracheal axis, but even in the small branches. (Fig. 11.) The epithelium of the tracheæ of the photogenic tissue is altogether different from that figured by Wielowiejski for *Lampyris*. Instead

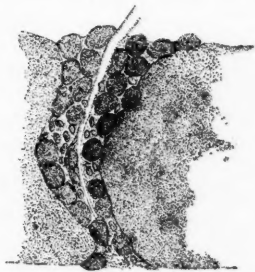


FIG. 9.—Section parallel to axis of cylinder. Herman's fluid.  $\times 235$ .

of being thick, it is very thin, with large flattened nuclei. In both longitudinal and transverse sections, where a nuclear stain has been used, the epithelium may be readily traced within the cylinders, even to the finer branches. It is exactly similar in appearance to that in the dorsal layer, and is wholly distinct from the cellular elements of the cylinder. Small flat nuclei are seen closely applied to the tracheæ, while the irregular nuclei of the cylinder cells lie at a little distance away.

In his study of *Luciola* in 1886, Wielowiejski did not find the cylinder a syncytium, as stated by Emery, but believed it to be composed of two elements, a nucleated epithelium immediately surrounding the trachea, and an outer layer belonging to the parenchyma. The latter he found generally separated from the trachea by the action of reagents, but still connected with the parenchyma cells. These observations would seem to be in agreement with the conditions found in *Photinus*.

The bulk of the cylinder is thus shown not to be of tracheal origin. The tracheæ pass into the cylinder cells, there dividing to form the tracheoles, so that the name "transition cells" is equally befitting here, although the structures to which it is applied cannot be considered homologous with those of the "capillary end-network" of the caterpillar. If the cylinders belong to the parenchyma, they are at least clearly distinguished from it by definite boundary lines. In some cases there might seem to be a transition between the cells of the dorsal layer and those of the cylinder, but the cylinder cells are much smaller than those of either the dorsal layer or the parenchyma. They retain their spherical shape much more than either of the others mentioned. It would seem probable that all

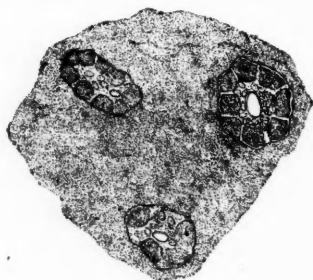


FIG. 10.—Section transverse to cylinder. Herman's fluid.  $\times 235$ .

cylinder a syncytium, as stated by Emery, but believed it to be composed of two elements, a nucleated epithelium immediately surrounding the trachea, and an outer layer belonging to the parenchyma. The latter he found generally separated from the trachea by the action of reagents, but still connected with the paren-

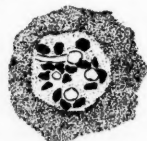


FIG. 11.—Section through cylinder showing epithelium of trachea.  $\times 235$ .

three forms of cells are of the same origin and that their structural differences are due to difference in function.

Wielowiejski, from his work on *Lampyrus splendidula* believed in the possible transformation of the parenchyma cells of the ventral layer into the cells of the dorsal layer through the physiological effects of photogeny. Emery did not accept this theory, and after his study of *Luciola* and two American species of *Lampyridæ*, Wielowiejski himself ('89) stated that, for those forms at least, it was untenable.

The conditions in *Photinus* are such as to apparently preclude such an hypothesis. The two layers are distinctly separate in all preparations and the relative thickness of the layers is fairly constant. There is no indication of a transition between the two layers, nor is there any apparent difference in the thickness of the layers in material put up in early summer and in that taken at the close of the flying season. Still more important are the inherent differences in the two layers. In the dorsal layer there is a solid mass of polygonal cells, similar in form and size, and irregularly penetrated by tracheæ. In the ventral layer there is a distinct division into two elements, the cylinders enclosing the tracheal trees, and the parenchyma cells. The arrangement and distribution of the tracheæ of the ventral layer is strikingly regular. The parenchyma cells are extremely irregular, both in form and size. It would, therefore, seem difficult to suppose that the dorsal layer could grow at the expense of the ventral layer.

Several theories have been offered as to the origin of the photogenic tissue. Kölliker ('57) regarded the light organs as "nervous apparatus." Owsjannikow ('68) thought them of epithelial origin. Wielowiejski ('86) suggests their derivation from the "kleine Ænocyten" which he finds absent in the photogenic species of *Coleoptera*. The most general view, however, is that the photogenic tissue is differentiated fat body. This is upheld by a general similarity in structure, position and cell content. It has been already noted that granules exactly similar in appearance to the urate crystals of the dorsal layer have been found in the fat body near the light organs.

A question of this character could be settled only by onto-

genetic study of the photogenic tissue. This has not been attempted, so far as I can learn, by anyone besides Dubois ('98). He has studied the development of both *Lampyrus noctiluca* and *Pyrophorus noctilucus* from the earliest stages. The eggs were found to be luminous even before they were laid, so that the light was transmitted in unbroken continuity from one generation to the next. Dubois followed the development of the light organs through all the different changes occurring from the beginning of segmentation to the emerging of the adult insect, and his observations led him to state definitely that the photogenic tissue is derived directly from the underlying hypodermis, by a proliferation of these cells. He also states that in the development of the organs a transformation takes place in the protoplasm of the cells, the older cells toward the upper surface of the light organs becoming filled with opaque, chalky granules. The younger cells, in which this transformation has not taken place, constitute the parenchyma.

While these results are not in line with previously accepted ideas in regard to the derivation of the light organs, they are based upon the only kind of study which can determine the problem. Apparently Dubois's work has not been generally accepted, and it needs verification by other workers. Nothing could be more profitable in our present state of knowledge than extensive and thorough study of the photogenic tissue throughout all its transformations.

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ORAL BREATHING VALVES OF TELEOSTS,  
THEIR MODIFICATIONS AND RELATION  
TO THE SHAPE OF THE MOUTH.

EVELYN GROESBEECK MITCHELL.

ALTHOUGH the oral breathing valves of teleost fishes are very prominent and their function important, they have, strangely enough, been almost wholly neglected. Owen ('66), suggests that they "seem intended to prevent the reflux of the respiratory stream." Macallum ('84) mentions them in his article on *Amiurus* but ascribes to them no function. Stannius ('39) has described them, as has also Cuvier ('36) who suggests that they not only prevent the reflux of water but the escape of food. Galton ('71), describes the valves and their working in detail, much as Dahlgren ('98) did later. Howes ('83), refers to them in the trout, explaining their function.

In 1898 Dahlgren, who knew nothing of Galton's article,<sup>1</sup> took up the subject in detail and describes the valves in the sunfish, *Eupomotus gibbosus*. The valves are sheets of membrane composed of elastic connective tissue covered with a mucous membrane continuous with that lining the mouth. They are situated in the oral cavity just caudad of the maxillary and mandibular teeth. In this species of sunfish there is a median muscular thickening. The valves "are placed with their edges pointing downward and backward at an angle of less than forty-five degrees to the axis of the body. This angle is increased to about eighty degrees when the valves are struck by the regurgitating stream of water."

The function of the oral valves is to aid in the act of breathing, which has hitherto been described as "a kind of swallowing."

Dahlgren says, "The respiratory stream enters the oral cavity by the mouth and leaves by the two gill openings." . . . .

<sup>1</sup> His attention has since been called to it by the present writer.

"In inspiration the stream enters at the mouth in response to a dilation of the oral cavity produced by the outward lateral movement of the opercular frames.

"At the same time water is prevented from entering at the gill openings by the branchiostegal valves which although they are attached to the opercular frames, move independently of and contrary to them; so that, while this outward movement of the frames extends the gill openings, the branchiostegal valves close them automatically by the action of the water which tries to enter.

"In inspiration the water is forced out of the gill openings by a corresponding contraction of the oral cavity. At the same time the water is prevented from regurgitating through the mouth, not by the contraction of the latter, but by the automatic operation of the maxillary and mandibular breathing valves which move as accurately and efficiently as any of the heart's valves. Caught on their posterior edges by the first movement of regurgitation, they snap together and completely prevent the water from leaving the oral cavity by the mouth which, meanwhile, is left partly open, almost as much open as during inspiration.

"That these valves are of value as breathing organs is evident upon casual observation; that they are of much importance is shown by the compensatory action, brought about by injury; that they are not of immediate vital importance is proved by the fishes' ability to get along without their services until they are repaired."

In examining about 70 species of fishes, the writer finds two types of valves. These she has called the crescentic and the U-

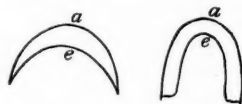


FIG. 1.—Types of valves. C, crescentic; U, u-shaped type. a, attachment; e, free edge.

shaped types. (Fig. 1.) There is a third form which may, however, be considered as a modification of either type and will be described later.

The crescentic type of valve is typically shown in the catfishes, Siluridæ, particularly in *Schilbeodes punctatus*. This type of valve, as its name indicates, is in the form of a crescent with tapering ends, and may be broad or narrow. That of *Eupomotus gibbosus* is also of this type. The

free edge of the crescent is not necessarily a perfect curve (Fig. 2, *a*), but may be interrupted by a projection or a notch. (Fig. 2, *b*, *c*, *d*.)

In the U-shaped type, the ends do not taper but are bluntly truncate. (Fig. 1, *u*.) The free margin in these also may be perfect or interrupted.

A number of interesting modifications occur. As before mentioned, the free edges are often interrupted

and in some cases, as in *Pomolobus pseudoharengus* and *Pomolobus æstivalis*, are attached near or at the meson, in one or two lines, to the roof of the oral cavity. (Fig. 3.)

The central thickening which Dahlgren mentions may be a tooth-like projection, may extend only halfway to the free margin or back between the tooth pads, may be straight, wedge-shaped, semi-circular (in this case the flat side was against the attachment), or may be round, this form being either at the meson on

the attachment or in the center of the valve. (Fig. 4.) In one case, that of *Ameiurus natalis*, a horizontal thickening passed through the round centrally situated, mesal thickening. (Fig. 4, *j*.) The thickenings may be found in either or both valves. They appear to be muscular. Their function may be to strengthen, possibly to tighten, the valves, as they are found on the

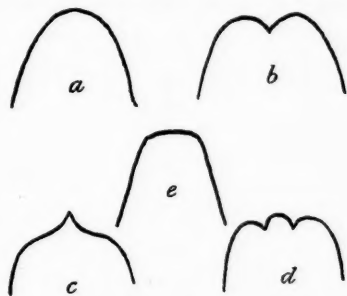


FIG. 2.—Forms of free margin. *a*, perfect; *b*, projection; *c*, notched; *d*, fastened each side of meson; *e*, squared

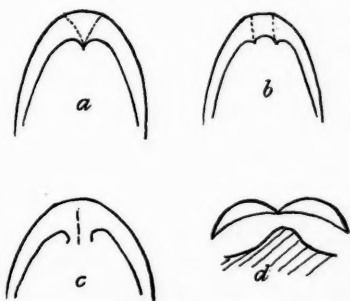


FIG. 3.—Attachment of free edges of maxillary valve at or near meson. *a*, *Clupea pseudoharengus* (v-shaped attachment); *b*, *æstivalis* (parallel attachment); *c*, *Dorosoma* (median linear attachment); *d*, *Astroscopus* (median point attachment).

larger valve when the valves are of unequal size, and this valve

is the more subject to strain and injury from its size and position. What is meant by "position" will be explained in the

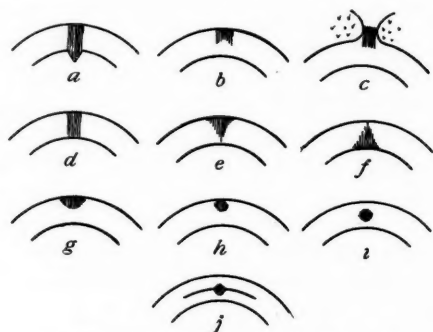


FIG. 4.—Forms of central thickenings. *δ*, tooth-pads.

paragraph on the relationship of the valves to the shape of the mouth.

In the majority of species examined, papillæ are found on the valves. These papillæ vary widely in size and arrangement.

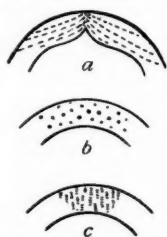


FIG. 5.—Some typical arrangements of papillæ. *a*, in lines; *b*, irregularly scattered; *c*, in short rows so that they resemble a number of small thickenings or folds.

They may be in almost regular rows, scattered, cover the whole valve or only a part of it, even, as in *Cynoscion nebulosus*, run back among the teeth. They may be coarsely setiform, flattened, rounded, on a stalk or, in one case, of a circumvallate appearance. (Figs. 5 and 6.) In some cases the papillæ are fine and closely arranged in rows, giving the appearance of short vertical rows or folds. (Fig. 5*c*.) These are easily distinguished from the true folds found on some valves. These papillæ at first appeared to be one elongated papillus but proved to be

as described. In *Amblopytes gruniens* are found rugæ surmounted by small papillæ.

A third kind of valve has been mentioned as being a modification of either the crescentic or U-type. The writer was for a long time greatly perplexed because many of the Cyprinidæ

apparently had no mandibular valve, yet, from the shape of the mouth, there was every reason to expect a small one. Finally in a large specimen of *Semotilus atromaculatus* it was seen that the place of the valve was taken by several rows of tall papillæ. (Fig. 6, *d*.) This was found to be the condition in all the minnows where the mandibular valve seemed absent.

The function of the papillæ may be to aid in the finding of food. The best development of papillæ seems to be among the bottom feeders, where such sense organs would be most useful. Another modification of the valves is in the pigment which is frequently found in one or both valves. The pigment spots may be regularly arranged or scattered like the papillæ the arrangement varying with the species.

Some valves are further distinguished by rugæ or folds or by



FIG. 6.—Forms of papillæ. *a*, setiform; *b*, vertical section and surface view of the flattened papillæ; *c*, wounded; *d*, stalked. *e*, circumvallate.



FIG. 7.—Valves of *A. grunniens*. *a*, maxillary; *C*, mandibular.

very thin and transparent margins or both as in the case of *Ambloplites grunniens* (Fig. 7).

As before stated, the valves are not ever of quite equal size. Their size and shape are dependent on the size and shape of the mouth. For instance, in the case of the Siluridæ, (Fig. 8, *a*) the mouth is terminal, practically horizontal and very wide. For this reason it does not need to be opened far to admit the requisite amount of water, therefore the valves are long and crescentic but only of moderate depth, (*i. e.* the distance from attachment to margin). The mouth being horizontal, the regurgitated stream strikes the two valves with about equal force; therefore, both must be well developed.

In the Catostomidæ, or suckers, the case is very different. Here the mouth is inferior, (Fig. 7, *c*), and the snout depressed. In this family the maxillary valve is well developed and very deep. There are two reasons for this. First, the mouth of the sucker is not wide and must be opened farther; second, the lower valve is entirely absent. The reason for this is obvious. The depressed snout decurves the regurgitated stream, which strikes the upper valve only, hence a lower valve is not necessary, the edge of the upper valve catching against the lower jaw.

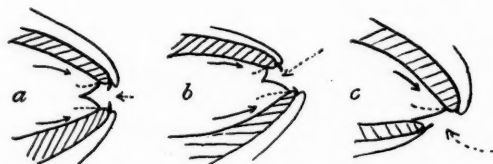


FIG. 8.—*a*, sagittal section showing incident and excurrent streams and position of valves when open and closed in horizontal mouth. *b*, similar section in superior mouth; *c*, in inferior mouth.

The position of the maxillary valve in these fishes is nearly horizontal, this being a better position to catch the returning stream. In the case of the minnows whose mandibular valve is replaced by papillæ, and in the case of some other fishes with maxillary valves much larger than the mandibular valves, the mouth is apparently horizontal or even slightly oblique. In all such cases, however, either the snout is depressed or the premaxillary is protractile and is held protracted when the fish is breathing quietly, thus depressing the snout and deflecting the greater part of the water against the maxillary valve.

As may be inferred from the foregoing, the fishes with true oblique mouths possess large mandibular and small maxillary valves. The latter are never completely absent but may be very small. The case of *Astroscopus y-græcum*, the "stargazer," might be supposed to form an exception to this rule, as the mouth is really superior. From analogy it might be supposed that the maxillary valve would be lacking. Such, however, is not the case. There is a well developed maxillary valve (Fig. 3), like two crescentic valves joined at the meson by their ends.

The reason for this structure is easily seen when the floor of the oral cavity is examined.

This floor is raised in the center and hollowed at each side in such manner as to divide the outgoing stream into two, and the corresponding part of the roof is so shaped and hollowed as to deflect the stream somewhat, so that notwithstanding the superior position of the mouth, the upper valve is necessary.

In *Echensis naucratis*, where the mouth is truly superior, there is a small maxillary valve, whose greatest width is on the parts each side of the meson about half way to the ends. This also can be accounted for by the hollowing out of the roof of the oral cavity.

In *Hemirhamphus unifasciatus* the mouth appears superior, but it is more truly horizontal, the appearance being produced by the great prolongation of the mandible. This species has the maxillary valve but little smaller than the mandibular.

*Pomolobus pseudoharengus* affords a very characteristic example of the development of the mandibular valve. The mouth being very oblique and narrow, the mandibular valve is very deep and "baggy." (Fig. 8.)

In *Chilomycterus schæpfi* the valves are crescentic, the mandibular valve being four times the width of the maxillary valve. The valves are covered with coarse papillæ. They entirely close the mouth when the jaws are at full stretch, which has been noted in no other species.

A good example of deep valves is found in *Oncorhynchus nerka*, a salmon. In this fish the jaws are hooked, long and somewhat compressed. If the valves were narrow, there would be a long, free margin. Consequently the valves would have to be very heavy to resist the outward pressure from within against the unsupported margins. As it is, the free edges lie far back in the mouth, their length is much reduced and the surface of the valve, which is far better able to stand the strain, increased and hung in a better position for resistance between the bones of the jaws. (Fig. 9.)

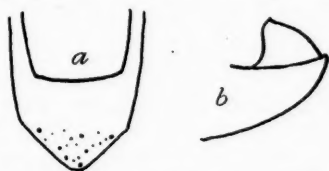


FIG. 8.—Mandibular V of *P. pseudoharengus*. *a*, from above; *b*, from the side.

The valves of predacious fishes seem to be the heavier and more strengthened by muscular thickenings. This may be because the feeding habits of such fish would be liable to injure the more delicate membranes.

The valves vary widely in different genera and in different species of the same genus. The generic variation depends on general shape, size and appearance; the specific on papillæ, muscular thickenings and pigment. The general type of a fam-

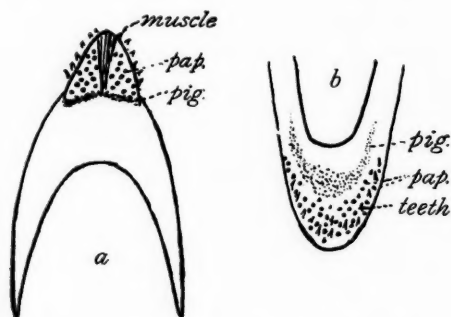


FIG. 9.—Valves of *O. nerka*. a, maxillary; C, mandibular.

ily, notwithstanding, is very characteristic, except, perhaps in the minnows, in some of which the papillæ form valve occurs. By general type, the general appearance is meant; not the crescentic or U-types only. Individual variation seems comparatively slight and generally resulting from injury. If one individual shows a certain arrangement of pigment, papillæ, and central thickening, it will, so far as it has been possible to ascertain, be found in the rest of the species and nowhere else. For convenience of comparison and explanation the writer has, where enough species and specimens were available, arranged results in synoptical form.

The writer desires to thank Dr. Burt G. Wilder and Dr. H. D. Reed for valuable hints and use of specimens and, more especially, for their kind interest and encouragement.



CATOSTOMIDÆ.

- A. Papillæ present.
  - B. Small papillæ in fold-like rows over whole valve  
*Erimyzon sucetta*
  - BB. Papillæ not in fold-like rows.
    - C. Papillæ on proximal half<sup>1</sup> of valve *Catostomus macrocheilus*
    - CC. Papillæ over whole valve.
      - D. Papillæ crowded over whole valve; distinct, rounded, not so large as those on lips . . . *Catostomus catostomus*
      - DD. Papillæ less crowded in distal<sup>2</sup> half or in a circular mesal spot.
        - E. Circular mesal spot where papillæ are flattened, small and well separated . . *Catostomus nigricans*
        - EE. No such spot. Proximal papillæ about size of those on lips and in several rows. Distal papillæ less crowded, flatter, rather elongate  
*Catostomus commersoni*
  - AA. Papillæ absent.
    - F. Small thickenings, perpendicular in direction, resembling long, low papillæ in appearance . . . . . *Moxostoma macrolepidotum*

SILURIDÆ.

- A. Papillæ on both valves.
  - B. Thickenings triangular and in Mand. V.
    - C. Thickening erect-triangular, (apex toward free edge)  
*Amiurus vulgaris*
    - CC. Thickening inverted-triangular, apex toward tooth pads.
      - D. Pigment on thickening and spreading in a crescent through the valve on either side . . *Noturus gyrinus*
      - DD. No pigment in either valve . . . *Noturus miurus*
  - BB. Thickening in Max. V. and not triangular.
    - E. Thickening a vertical rod. Papillæ on Mand. V. larger and closer set than those on Max. V. . . *Amiurus nebulosis*
    - EE. Thickening not a vertical rod.
      - F. Thickening shaped like a sphere with a rod running through it parallel to the free edge  
*Amiurus natalis* (Fig. 4, j.)
      - FF. Thickening spherical, barely touching attachment and covering  $\frac{2}{3}$  the width of the valve. Papillæ so small that the valves at first appear smooth, on proximal  $\frac{2}{3}$  of the Max. V. sparsely scattered on Mand. V.  
*Ictalurus punctatus*

<sup>1</sup> Proximal, — near or toward the attachment.

<sup>2</sup> Distal, — away from the attachment.

## AA. Papillæ on Mand. V. only.

Central muscular thickening passing between tooth pads

*Noturur flavus*

## CLUPEIDÆ.

A. Max. V. not attached mesally . . . . . *Clupea harengus*

## AA. Max. V. attached mesally.

## B. Attached on one perpendicular median line.

C. Mand. V. a crescent, wide; the distal two thirds thin and delicate, no pigment . . . . . *Dorosoma cepedianum*

CC. Mand. V. a horseshoe with pointed ends and the free margin rather squared off at the apex of the curve not perfectly curved like the attachment. Valve much wider at apical part of curve than on sides, (Fig. 2, s)

*Opistheoma oglinum*

## BB. Max. V. attached mesally on two lines. (Fig. a. b.)

D. Attachment V-shape. (Fig. 3, a.) *Clupea pseudoharengus*DD. Attachment in parallel lines, margin between ends of these lines free. (Fig. 3 b.) . . . . . *Clupea æstivalis*

## PERCADÆ.

A. Thickening in Max. V., a three quarters circle flattened against attachment and covering most of width of valve . . . *Perca americanum*

## AA. No thickening.

B. Papillæ and pigment . . . . . *Hadropterus aspro*

## BB. No pigment.

C. . . . . *Boleosoma nigrum*CC. . . . . *Etheostoma caprodes*

## CENTRARCHIDÆ.

## A. Max. V. extending between tooth pads.

## B. Papillæ in perpendicular rows on either or both valves.

## C. Rows ridge-like (or fold-like).

D. Ridge-like rows on both valves . . . *Amblopytes rupestris*

DD. Ridge-like rows on Mand. V. only

Pigment spots on the papillæ . . . *Micropterus salmoides*CC. Papillæ in rows on Mand. V. but not close enough to give ridged appearance. Slight thickenings in V. under the rows of papillæ. Clear margin . . . *Eupomotus gibbosus*

## BB. Papillæ not in perpendicular rows.

## E. Papillæ numerous on one or both valves.

F. Papillæ very large, flat and crowded on both valves, giving tessellated appearance, and extending between tooth pads . . . . . *Apomotus punctatus*

- F.F. Papillæ on Max. V. rather flat, medium size, crowded but not giving the appearance of those in F; a few pigment spots at meson; mesal fold *extending but slightly* between tooth pads.  
Mand. V. covered with fine rounded papillæ little crowded, pigment in proximal half. . . *E. auritus*
- EE. Papillæ few.
- G. A few large papillæ on Mand. V. along attachment; central thickening extends through tooth pad and half way to margin; well pigmented. Papillæ in Max. V. fine and well separated  
*Chænobrytes gulosis*
- GG. No papillæ in Mand. V. Mand. V. well pigmented at base, and meson quite black. Max V. well pigmented, especially between tooth pads. Papillæ few and small . . . . . *Pomoxis sparoides*
- AA. Max. V. not extending between tooth-pads.
- H. Papillæ in vertical, fold-like rows . . . . . *Apomotus pallidus*
- HH. Papillæ not in vertical, fold-like rows.
- I. Papillæ of Mand. V. very few and flat, hard to see. Those of Max. V. blunt setiform. Mand. V. well pigmented on proximal half . . . . . *Micropterus dolomieu*
- II. Max. V. with fine, rounded, evenly distributed papillæ and slight mesal thickening. Mand. V. with fewer and somewhat larger papillæ; a few pigment spots on base at meson extending through tooth-pads *Eupomotus holbrookii*

## ARGENTINIDÆ.

- Valves crescentic; no papillæ; mandibular valve somewhat the larger.
- A. Mesal thickening on mandibular valve circular in shape and placed against attachment of valve, covering about  $\frac{1}{4}$  the width of the valve. Central third of maxillary and proximal half of mandibular valve pigmented . . . . . *Osmerus mordax*
- AA. No mesal thickening.  
Pigment spots near attachment of mandibular valve, few and variable . . . . . *Hypomesus pretiosus*

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